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THE UNIVERSITY OF KANSAS
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VOL. XLII] DECEMBER 29, 1961 [No. 1

Weights of the Ventricular Walls of the Heart in the Adult Dog

BY

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ABSTRACT: The body weight, the weights of the entire heart and of the two ventricular walls, from a heterogeneous laboratory series of 15 male and 31 female dogs, have been studied statistically. The entire heart as a percentage of body weight and each ventricular wall as a percentage of total heart weight are presented. The ratios of the weight of the left ventricular wall to the right ventricular wall range from 1.80 in the females and also in the group of larger dogs to 1.84 in the smaller dogs and 1.87 in the males. These ratios are not statistically different and all of them fall well within the range of the reported ratios for the human heart.

INTRODUCTION

The ratios between the weights of the two ventricular walls have been a subject of investigation for over three quarters of a century, with most of the ratios based on the human heart. Müller in 1883 weighed and compared the right and left ventricular walls of the human heart, and his work has been followed by that of Lewis ('14), Herrmann and Wilson ('22), Jones ('53), Latimer ('53), Keen ('55) and others. The weight of the entire heart has been studied in the fetal, postnatal and adult periods in man and in animals, but far less attention has been paid to the weights of the ventricular walls.

The ratios between the weights of the ventricular walls in two inbred races of rabbits have been reported (Latimer and Sawin, '59) and these ratios are different, with the left wall significantly heavier, relative to the right wall, in the smaller and more active race. There is also a sex difference in these ratios of the ventricular walls in the larger race of rabbits but not in the small race. These differences in the ratios between the ventricular walls in the two

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races of rabbits suggest that similar differences might be found in the dog hearts. This report will show that although the ratios in male and female, small and large dogs do differ slightly, these differences are not significant. Also, all of these ratios fall within the range of the ratios reported for the human heart.

MATERIALS AND METHODS

The dogs from which these hearts were removed were a typical laboratory collection which had been used for only short experiments in the Physiology laboratory. There were 15 males and 31 females, all adults and ranging in body weight from 3.86 to 10.89 kilograms. The dogs were weighed on a platform balance sensitive to 0.25 pounds by the students as the initial part of the experiment, and these body weights in pounds were changed later to kilograms. The experiments never lasted over two hours and the dogs were sacrificed by additional anesthetic at the end of the experiment. The entire hearts, as soon as removed from the body, were placed in a moist chamber and dissected and weighed as soon as possible. All weights were made in the fresh condition and in the same manner as for the rabbit hearts.

Slightly different methods of dividing the human hearts are reported, but these dog hearts were dissected by one person and using the same methods employed in the study of the guinea pig (Latimer, '52), human (Latimer, '53) and rabbit hearts (Latimer and Sawin, '59). The method of removing the two ventricular walls has been described in detail in the earlier report (Latimer and Sawin, '59) and only the general plan will be described here. The great vessels were severed close to their emergence from the heart.

The free portion of the right ventricular wall was removed by an incision started by putting one tip of the scissors into the orifice of the pulmonary artery and carrying this incision toward the apex of the heart along the right side of the anterior longitudinal sulcus and close to the septal wall. This incision was carried around the apex of the heart and then along the posterior longitudinal sulcus as far as the coronary sulcus, following as closely as possible the junction of the interventricular septum and wall of right ventricle. Next the right ventricular wall was removed by making an incision just distal to the coronary sulcus and also distal to the attachments of the atrioventricular valves. Thus the right free wall was removed, leaving the atrioventricular valves attached to the remainder of the heart, and the papillary muscles attached to the free wall. The

chordae tendineae were separated from the papillary muscles at their junction. The free wall of the left ventricle was separated in a similar manner. This was a little more difficult for the left wall tended to curve around as it entered the septum. Corrections in this dissection, if necessary, were made after the cavity of the left ventricle had been opened. Then the two atria were opened and all contained blood was washed from all of the cavities with tap water. Next the two ventricular walls and the remainder of the heart, consisting of the interventricular septum and the two atria, were carefully dried on paper toweling. The three parts were weighed all together in glass-stoppered weighing bottles to obtain the weight of the entire heart. Then each ventricular wall was weighed separately while the remaining ventricular wall was kept in a moist chamber. All weights of the heart and the two ventricular walls were made on an analytical balance sensitive to 0.1 mg. but the weights were recorded only to the nearest milligram.

I wish to thank the Department of Physiology for permission to collect these dog hearts and the medical students who so kindly provided the body weights.

TABLE 1.—Weights, percentage weights and ratios of the right and left ventricular walls in entire group of adult dogs. All weights in grams except body weight in kilograms.

	Average and standard deviation	Coefficient of variation
Body weight	6.69 ± 1.53	22.90
Heart	55.58 ± 13.84	24.91
R. V. wall	12.22 ± 3.12	25.52
L. V. wall	22.17 ± 5.61	25.01
Ratio, L. V. W./R. V. W.	1.82 ± 0.205	11.23
Heart % of B. W.	0.843 ± 0.158	18.87
R. V. W. % heart	22.02 ± 1.64	7.47
L. V. W. % heart	39.48 ± 2.56	6.49

VENTRICULAR WEIGHTS IN ENTIRE GROUP OF DOGS

The body weight, weight of the entire heart and the weights of right and left ventricular walls are shown for the entire group of dogs, of both sexes, in the first 4 lines of table 1. The last 4 lines show the ratio of the weight of the left to the right ventricular wall, the weight of the entire heart as a percentage of body weight and the weights of each ventricular wall as percentages of total heart weight. The second column contains the average weights, the ratio of the two ventricular walls and the percentage weights to-

gether with their standard deviations, and the last column, the coefficients of variation.

The weights in grams of the two ventricular walls are the most variable followed by the weight of the entire heart and then the body weight. The heart as a percentage of body weight is, as expected, less variable than its weight in grams. Body weight is generally more constant than the weights of the individual organs. The lowest coefficients of variation are for the weights of the two ventricular walls expressed as percentages of total heart weight. The left ventricular wall comprises a larger proportion of total heart weight than the right ventricle and it might be expected to be less variable when expressed as a percentage of total heart weight.

The ratio of 1.82 between the weights of the two ventricular walls in these dogs is much like the ratios for selected human hearts (see Latimer and Sawin, '59, table 3).

SEX DIFFERENCES

The body weight, the weights and percentage weights of the heart and the two ventricular walls, and the ratios between the ventricles are shown in panel A of table 2. The averages and standard deviations for the 15 male dogs are shown in the second column and the coefficients of variation, in the third column. Similar data for the female dogs are found in the fourth and fifth columns, and the last column contains the "t" values of the sex differences. This last column shows but one measurement, the percentage weight of the entire heart with reference to body weight which is significantly greater at the 5% level in the male dogs. The body weight averages slightly heavier in the females and the weights in grams of the entire heart as well as both ventricular walls are slightly heavier in the male dogs and consequently it is to be expected that the percentage weight of the heart would be larger in the males. This is in agreement with the report of Northup *et al.* ('57), which will be discussed in a later section.

The least sex differences are in the body weight and in the weights of the two ventricular walls as percentages of total heart weight, with the percentage weight of the right ventricle manifesting the least sex difference of any of the measurements in panel A.

Possibly the heterogeneity of this small group of dogs may have something to do with the lack of sex differences in these measurements, for the only significant sex difference is in the percentage weight of the entire heart. The differences in the ratios between

the two ventricular walls are very slight, but the males do have slightly heavier left ventricular walls compared with the right walls.

TABLE 2.—Weights, percentage weights and ratios of ventricular walls in male and female, and in large and in small dogs. Weights in grams except body weight in kilograms.

	Average and standard deviation	Coefficient of variation	Average and standard deviation	Coefficient of variation	"t"*
Panel A	15 males		31 females		
Body weight	6.61 ± 1.30	19.70	6.72 ± 1.65	24.48	0.24
Heart	59.60 ± 14.74	24.72	53.63 ± 13.22	24.64	1.37
R. V. W.	13.13 ± 3.38	25.74	11.78 ± 2.95	25.00	1.37
L. V. W.	23.68 ± 6.04	25.50	21.11 ± 5.24	24.81	1.47
Ratio, L. V. W./R. V. W.,	1.87 ± 0.206	10.98	1.80 ± 0.204	11.35	1.09
Heart % body weight	0.913 ± 0.184	20.20	0.809 ± 0.136	16.75	2.14
R. V. W. % heart	22.01 ± 1.22	5.52	22.03 ± 1.83	8.30	0.04
L. V. W. % heart	39.77 ± 2.86	7.18	39.34 ± 2.45	6.22	0.53
Panel B	22 small dogs		24 large dogs		
Body weight	5.41 ± 0.78	14.49	7.86 ± 1.06	13.53	8.83
Heart	47.75 ± 9.10	19.05	62.75 ± 13.98	22.28	4.27
R. V. W.	10.59 ± 2.26	21.33	13.71 ± 3.15	22.98	3.83
L. V. W.	19.01 ± 4.07	21.40	24.64 ± 5.58	22.65	3.88
Ratio, L. V. W./R. V. W.,	1.84 ± 0.239	12.95	1.80 ± 0.177	9.82	0.62
Heart % body weight	0.887 ± 0.132	14.90	0.802 ± 0.175	21.83	1.84
R. V. W. % heart	22.20 ± 2.04	9.19	21.86 ± 1.24	5.69	0.71
L. V. W. % heart	39.69 ± 2.64	6.65	39.29 ± 2.59	6.59	0.52

* The "t" values in panel A of 2.14 and above are significant at 5% and 2.98 and above are significant at 1% and similar "t" values in panel B are 2.08 and 2.83 respectively.

DIFFERENCES DUE TO BODY SIZE

All of the dogs, irrespective of sex, were grouped according to body weight in panel B, table 2. All dogs below average body weight were placed in the first group, and those above, in the second group and data, arranged as in panel A, are given for these two groups. In these two groups, selected for body size, one would expect that the "t" values of the differences in body weight and in the weight of the heart and its ventricles, would be significantly different, as shown in the first four lines of panel B. The ratios of the weights of the two ventricular walls and the three percentage weights, however, are not significantly different. Thus the size of the dog does not significantly affect the ratio of the weight of the left ventricular wall to that of the right wall. The percentages of total heart weight are not significantly affected by the body weight, but the heart tends to be slightly larger, as a percentage of body weight, in the smaller dogs.

Although the ratios between the two ventricular walls are not

significantly different in the two panels of this table, yet the ratios are somewhat larger in the males and in the group of smaller dogs. The size of the dog, however, does not affect the relative weight of the heart nor its proportions as much as does the sex. These dogs were mongrels and possibly if they had represented two pure breeds of differing size and activity, similar to the rabbits, they might have shown differences in the proportions of the heart, especially if the two breeds represented different degrees of activity and corresponding differences in muscular development.

DISCUSSION

The primary interest in this study is in the weights of the two ventricular walls rather than in the weight of the entire heart. However, a recent report on 346 adult dog hearts by Northup *et al.* ('57) shows that the dog hearts are relatively larger in the males and also in the smaller dogs. The only significant sex difference in panel A, table 2 shows that the heart forms a larger percentage of body weight in the males than in the females, and the hearts, likewise, are relatively larger, although not significantly larger, in the smaller dogs (panel B).

Slightly different methods of apportioning the weight of the interventricular septum have been employed in some of the studies on the human heart. It has been divided in different ways between the weights of the two ventricular walls (Lewis, '14 and Herrmann and Wilson, '22); weighed entirely with the left ventricle (Keen, '55); or only the free ventricular walls have been removed for weighing and all of the septum left with the remainder of the heart. The interventricular septum does contribute to the function of both ventricles, but the weights of the free ventricular walls are more easily and exactly determined and they evidently give as accurate a measurement of the relative weights of the two ventricles as the methods which attempt to apportion the weight of the septum between the two ventricles. Especially in these smaller animal hearts, it would be very difficult to accurately apportion the septum into its right and left portions. The method of weighing only the two free ventricular walls seems to be the method of choice, especially for these animal hearts, and it has been used for some of the studies of the human heart (Fulton *et al.*, '52, Jones, '53 and Latimer, '53) and for all of the animal hearts.

Table 3 of a previous report (Latimer and Sawin, '59) shows the ratios of the weights of the left to the right ventricular wall for a few human and animal hearts. The range of these ratios is from

1.52 to 2.27. The ratios of the weights of the ventricular walls in carefully selected human hearts range from 1.74 to 2.00, and within this range fall the ratios for the entire group of this present series of dogs (1.82) and also the ratios for the groups of dogs as shown in table 2 (1.80, 1.84 and 1.87). The average of all of the ratios in this table of the preceding report is 1.92 or but 0.10 greater than the ratios for all of the dog hearts taken together (table 1).

The relationships of the weights of the two ventricular walls in this random collection of dogs is very similar to that reported for the guinea pig heart, for the similar ratio for a series of 100 guinea pigs (Latimer, '52) is 1.96 or but slightly higher than that of these dogs.

The only known data on the weights of the two ventricles in the dog are presented in a very brief report by Pembrey ('28). He lists the weights of the right and left ventricles in 5 puppies, one day old and all from one litter. Three puppies have heavier left ventricular walls, and in the other two the right ventricle is heavier. Averages of his weights show that the left ventricle weighs 85.4 and the right, 82.4 Cg. The sexes are not given nor the methods of dissection. Evidently these newborn puppy hearts had not attained the adult proportions of the two ventricles, and so far as is known the time of this change has not been determined.

There is no significant sex difference in the ratios of the ventricular walls in these dogs although the ratio is slightly larger in the males. Unlike the dogs, the rabbits have relatively heavier left ventricular walls in the females. In the race of large rabbits the ratios are 1.69 for the females and 1.52 for the males, or significantly less in the males. The race of small rabbits however manifest no significant sex difference although the females have a slightly larger ratio.

The minimum ratio in the table of the preceding report is 1.52 for the males of a race of large and inactive rabbits (race III) and the similar ratio, also in the males, in a race of small and more active rabbits, is 2.03 and this larger ratio is significantly larger than the ratio of 1.52 for the large males. Likewise in panel B, table 2 the ratio for the smaller dogs is slightly but not significantly larger than in the large dogs.

In conclusion, these dogs do not show the significant differences in the weights of the two ventricular walls in the two sexes nor in the small and large dogs, which were so evident in the two races of rabbits. Possibly racial differences of body size or of activity are masked in this heterogeneous group of dogs. Differences in pro-

portions between the two ventricular walls similar to those reported for the rabbits might be found in groups of purebred dogs of differing size and degrees of activity, but they are not evident in this present collection of mongrel dogs.

SUMMARY

Body weight, the weights of the entire heart and of the two ventricular walls are presented, together with the ratios between the weights of the two ventricular walls, the weights of the heart expressed as a percentage of body weight and the weights of the ventricular walls as percentages of total heart weight. The weights of the ventricular walls and the total heart weight are the most variable, with the percentage weights of the two ventricular walls the least variable and the ratios between the weights of the ventricles slightly more variable.

The ratio of the weight of the left ventricular wall to that of the right in all the dogs together is 1.82, which is well within the range of the published ratios for man and animals.

The heart as a percentage of body weight is significantly larger in the males and this is the only significant sex difference in these data. The ratio of the ventricular walls is 1.87 in the males and 1.80 in the females. This difference is not significant.

Again these dogs were divided, irrespective of sex, into a group of small, and a group of large dogs. Naturally, the observed weights are significantly different, but the ratios and all of the percentages give no evidence of significant differences. The ratios of the weights of the ventricular walls are 1.84 in the small dogs and 1.80 in the large dogs.

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Studies in Behavior and Phylogeny of Certain New World Jays (Garrulinae)[1]

BY

JOHN WILLIAM HARDY

ABSTRACT: The behavior of certain species of jays is described, and differences and likenesses of behavior used to supplement knowledge of anatomy; a wider base for making a classification of New World jays is thus provided, one that more nearly reflects evolutionary relationships.

The Blue Jay (*Cyanocitta cristata*) and the Mexican Jay (*Aphelocoma ultramarina arizonae*) are discussed and compared as to degree of sociality and other aspects of behavior. The former species is territorial and flocks loosely in the nonbreeding season. The Arizonan Mexican Jay is highly social at all seasons; both the parents and other jays (some with parti-colored bills and of nonbreeding status) care for a single brood. The two species differ in other behavioral as well as morphological aspects.

Whereas Steller's Jay (*C. stelleri*) is much like the Blue Jay in habits, most races of the Scrub Jay (*A. coerulescens*) are unlike the congeneric Arizonan Mexican Jay, being highly territorial and showing no prominent age dimorphism in bill coloration.

Territoriality and narrowness of ecological adaptability probably are directly related, as indicated by comparison of the Mexican and Scrub jays.

Excluding *Gymnorhinus* and *Cyanolyca* from consideration, two tribes of New World jays are proposed to exist: an "Inornate line," Aphelocomini (containing only *Aphelocoma*), and an "Ornate line," Cyanocorini. Each "line" is characterized by patterns of plumage and behavior.

The relationships of age dimorphism in bill color and sociality are discussed from an evolutionary and a functional standpoint. A high degree of sociality is thought to be more primitive than territoriality of pairs in New World jays. All highly social species exhibit prominent age dimorphism of bill color, parti-colored bills, exteriorly, distinguishing sub-breeding status and, often, "helper" status in the breeding season. In less social species the bill is parti-colored exteriorly only prior to postjuvenal molt, although remnants of parti-coloredness persist on the interior surfaces of the bill for a longer period.

1. Submitted as a dissertation to the Department of Zoology and the Faculty of the Graduate School of the University of Kansas in partial fulfillment of the requirements for the degree of Doctor of Philosophy, in May, 1959.

Individuals of forms that are becoming less social possibly mature more quickly than others and exteriorly lose the parti-colored pattern of the bill earlier; maturity and exteriorly parti-colored bills in postjuvenal birds seem socially incompatible. In the Mexican Jay, the subspecies *arizonae* is highly social and possesses prominent age dimorphism in color of bill; subspecies *couchii* is less social, and the parti-colored condition of the bill disappears while the young are in the nest.

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INTRODUCTION

The studies reported in this paper were conducted with the aim of contributing to the understanding of behavior in New World jays. Particular attention was given to study of social behavior of members of the genera *Cyanocitta* and *Aphelocoma*. An attempt was also made to contribute to the concept of phylogeny of these jays through studies of their behavior.

There are but two extensive, published accounts concerning behavior of a New World jay, that of Amadon (1944a) on the Florida Scrub Jay (*A. c. coerulescens*) and that of Gross (1949) on the Mexican Jay (*A. ultramarina arizonae*). Rand (1937) raised fledgling Blue Jays (*C. cristata*) and wrote on their behavior. Scattered notes on behavior in jays of the genus *Aphelocoma* are to be found in Pitelka's (1951) systematic study of that group. Bent's (1946) summaries of the life histories of the North American species of jays reveal the paucity of information on behavior of jays.

Studies of five species of jays were conducted in the course of my work. These species are the Blue Jay (*Cyanocitta cristata bromia*),

Steller's Jay (*C. stelleri macrolopha*), the Scrub Jay (*Aphelocoma coerulescens woodhouseii*), the Mexican Jay (*A. ultramarina arizonae*), and the Magpie-Jay (*Calocitta formosa colliei*). Because of convenience, most information was gathered concerning the Blue and Mexican jays. The former is common in eastern Kansas where I reside, and the latter is common in the oak woodlands at the Southwestern Research Station of the American Museum of Natural History, where I spent two months of the summer of 1956 and a week in early spring of 1958. Limited studies were conducted of early phases of the nesting cycle of Scrub Jays in the Sandia Mountains near Albuquerque, New Mexico, and of wintering populations of that species in Oklahoma. Casual observations of Steller's Jay were made in the Chiricahua Mountains and elsewhere. In addition, observations of Magpie-Jays in Sonora and Sinaloa, Mexico, have provided information that may aid in better understanding the relationships between *Aphelocoma* and *Cyanocitta* and between these two genera and other New World jays.

The study here reported was divided into two major parts, (1) observation of jays in the wild and (2) observation of captive jays. Captives were confined in outdoor cages at Lawrence, Kansas, and for most of my stay at the Southwestern Research Station birds were kept in small indoor and outdoor cages for various purposes.

It does not seem probable that the behavior patterns common to most of the members of the family Corvidae occur fortuitously in so many species; these patterns may, therefore, be considered homologous characters, correlated with a common ancestry for members of the family. I am concerned primarily with considerations of the adaptive value of the behavior of *Aphelocoma* and *Cyanocitta,* some characteristics of which may be of systematic importance at the generic level.

METHODS OF STUDY

An attempt has been made to make all my observations comparative. "Knowing" what to look for in a species can, of course, be a hindrance, in that one may see only what he expects to see and remain unaware of habits outside the realm of his previous experience. I have attempted to guard against this pitfall, while comparing habits of birds that I was observing with those of species that I had studied previously.

In the wild, jays are easily observed, their nests found with ease compared to those of many other passerines, and, although

the birds are often quiet in the breeding season, they are not shy. Therefore, blinds are ordinarily neither necessary nor particularly useful. A blind was employed twice at nest-sites near pathways that persons used; jays at these nests were furtive and seemed to behave unnaturally when I was not concealed. As a rule, I was able to observe what I considered to be normal behavior by remaining motionless at the maximum distance that allowed me to watch whatever activity was taking place. Considerable movement on my part was sometimes necessary, because the range of individual birds or flocks is typically great even within a short space of time embracing one activity.

When nesting activities of a population of jays were observed, the nests were given designations consisting of N plus a numeral; thus, N-1, N-2, N-3. These and similar designations will be used in this paper where appropriate.

Captive jays were marked with colored plastic bands. The approximate age of the captives, sex, breeding condition, and state of molt were noted upon capture. Adults and juveniles were confined in outdoor cages six feet in height by nine feet wide and twelve feet long. One end of each of these cages was protected from rain and wind by canvas siding and woody shrubs placed inside. Roosting and other perching places, food and water were provided. Food consisted of nuts, acorns, sunflower seeds, millet, milo, melon seeds, bread, occasionally fruits such as grapes, and a generous supply of raw ground horse meat or commercial dog food. A regular supply of raw meat insured longer average life of the captives.

Jays captured as adults do not adjust well to captivity. Mexican Jays adapted much more readily to cage life than did Blue Jays. In fact, studies of the latter species in captivity were for the most part limited to observations of fledglings. No adult jays ever became so accustomed to captivity that they were not excited by the presence of people. Captives were handled as little as possible because of their excitability. I first made an attempt to "tame" them by remaining quietly in the cage for periods of several hours, but this method did not prove effective. Successful observations could be made only from a distance or, with caution, from a blind. A small blind was erected at the side of each cage. Even with this arrangement, the captives remained uneasy long after the observer had entered the blind.

Young jays of three species were raised from middle or late nestling stage to fully grown, flying stage (usually through the

postjuvenal molt). The three species were the Blue, Steller's and Mexican jays. These birds were retained in small cages approximately two feet long by one foot wide, by three feet tall. The birds were frequently allowed the freedom of closed rooms.

Experimentation was not a major part of the study, but opportunities to study the social and individual reactions of jays to artificially imposed stimuli, resembling certain natural stimuli, were utilized. Such experiments were carried out with both wild and captive, adult and young birds.

ACKNOWLEDGMENTS

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PART I.—BREEDING BEHAVIOR

Courtship Behavior

Early Courtship in the Blue Jay

Warm days in middle and late February usually are correlated with at least temporary abandonment of the winter habits in the Blue Jay and the assumption of a peculiar kind of flocking that seems to be in part socially and in part reproductively motivated.

Such flocking is a phenomenon transitional from nonbreeding to breeding phases of the annual cycle.

These early courtship flocks are composed of members of the wintering population and typically consist of from three to six birds. Collecting individuals from these groups, which persist into early May, indicates that they are composed principally of adult males. There is usually one female in each flock, pursued by the males. The behavior of the sexes in such groups is distinct enough that one can predict accurately the sex and age of each bird in the flock.

In middle and late May when nesting activity is well underway, there are still a few groups of jays flying about, performing in precisely the same manner as the adults in early spring. However, these birds are first-year birds and seem to be nonbreeders. They engage in courtship activities into early summer. The basis for stating that the first-year birds are nonbreeding individuals is that nesting records of Blue Jays at Lawrence have been those of adults (second-year or older) with only one exception; in 1957, I recorded the successful nesting of a pair in which the female was a first-year bird. According to Hickey (1952:119) pairs of Blue Jays both members of which were first-year birds have been observed in the act of copulation. Laskey (1958:213) records a first-year female that nested, using the previous year's nest of its parents and laying five eggs. The bird nested later in the year than adults. Probably the first-year birds that nest are among those which, like many adults, do not migrate. My record of the first-year female nesting was among the earliest nesting records of the 1957 season at Lawrence; the nest was begun in April at about the time that migrant Blue Jays are beginning to arrive in this region. The young in this nest were about a week old on May 25—a date when flocks of first-year birds were flying about the area in courtship flocks.

As Bent (1946:34) has noted, there usually seems to be in courtship flocks one bird, the female (?), which governs the activity of the group in courtship. When she flies, the others follow her in straggling formation; if she remains still, they do likewise; if, upon alighting, she hops upward among the branches of a tree, the others follow, continually attempting to be nearest her and occasionally even attacking each other.

In the early group courtship ritual, *bobbing* and flight displays are frequent. *Bobbing* is a distinctive courtship display of this and other species of jays. In *bobbing*, a bird moves its entire body quickly up and down several times, accomplishing this by flexing

and extending the legs at the ankle joint. As Tyler (*in* Bent, 1946:34) notes, this action is not bowing, since the whole bird moves up and down in approximately the same plane. In group display, all birds bob at once, although not in synchrony. One male seems to initiate such *bobbing* each time, after which the activity endures among all birds in the group for no more than three seconds. This is an erect display; the tail is fanned, the crest and head erected, and the body held rigidly upright with feathers closely appressed. The birds sit quietly or give the medium intensity *jayer* call discussed below. They remain in this tense state until suddenly one gives the "pumphandle" call, *cleeop cleeop,* or sometimes a rattling call, *br'r'r'r'r,'* and bobs vigorously up and down. The other jays in the group then also bob. The *cleeop* note is bell-like and not unlike a note of the Cowbird (*Molothrus ater*) in its liquid quality. It is used in low intensity phases of predator intimidation, in intimidation of fellow jays, as in the present instance, and in territorial skirmishes. It is nearly always accompanied by the *bobbing* display. The *br'r'r'r'r'* call resembles the sound made by a stick caused to vibrate against the edge of a table. It is uttered with the bill slightly open and seems to originate deep in the upper chest cavity. This call seems to be associated with anxiety, but I am not able definitely to categorize it. I have heard the call at all seasons of the year. It is given by both sexes and is often accompanied by *bobbing*, as in these courtship flocks. What may be an homologous call in the Brown Jay (*Psilorhinus morio*) is produced in the perhaps unique furcular pouch of the interclavicular air sac (Sutton and Gilbert, 1942:161). No such pouch is apparent in the Blue Jay. Figure 1 depicts a typical group of Blue Jays in courtship.

In flight from one station to another, and as the birds move about through the branches of a tree, the call, *wheedle-eee,* is often uttered, expressing the anxiety of the males. This "squeaky-gate" call resembles also the sound made by a clothesline on a pulley. It seems always to be associated with uncertainty or suppressed excitement. It is never given in association with the flight display.

Flight display (Fig. 3) is frequently engaged in by all members of the group (except when the female takes the lead in flight; then, the other members of the flock forsake display in order quickly to give chase). In full display, wings are held stiffly extended and widely spread, the head directed straight forward (it often is held bill downward otherwise), and tail widely spread. Both the *jaaay* and the *jayer* are given by the jays when in flight display.

Both calls are assembly calls that closely resemble the alarm calls; they are, however, less intensely given and do not connote danger.

On April 21, 1955, I observed three Blue Jays engaged in display that was slightly different from the above. In this case, the birds alighted in a row on a limb. The two outside birds began *bobbing* while the bird in the center remained nearly motionless. As the two bobbed, they gave the *cleeop cleeop* call. After about three minutes, the birds flew off, giving the medium intensity *jaaay*. Thus, in some instances not all birds in the group bob. Occasionally, I was not able to detect a leader among the birds, that is, one toward which *bobbing* was directed or which caused flight of the group. In the majority of cases, however, all birds bob, and one bird seems to be a leader.

The area covered by a courtship flock of Bue Jays is about one-quarter mile in diameter. In this area the flock moves freely, sometimes covering the distance from side to side in a single flight and never remaining in one place for over five minutes. Such groups are in evidence only in the morning hours, from daybreak until, usually, about 9:30 a. m., or slightly later on cloudy days. Once a group forms for the morning activity, it seems not to change in size or membership.

Group courtship probably functions to synchronize the reproductive states of the several jays in the flock; the birds gradually change from winter habits to intense courtship. Although I have watched these flocks carefully, I have never observed birds in them that I knew to be paired or members of pairs. Occasionally I have seen mated birds investigate these flocks, but they never join in the display.

Pair formation also seems to occur in these courtship flocks. Along with *bobbing* and flight display, there are aggressive movements and sometimes fighting among the males in their attempts to be near the female and prevent the other males from being near her. Through aggression and sometimes fighting, one male eliminates the others (or perseveres the longest) and becomes mated with the female member of the flock. The eliminated males then join or form other flocks, group courtship continuing until most adult members of the population are paired. In the subsequent phases of courtship next to be described, it will be noted that later courting groups usually consist of two or three birds—evidence that the number of competing males in a given flock gradually decreases.

I am convinced that there are birds, probably always adults, that never take part in activities of courtship in a given year. These birds are already mated, or in the late stages of becoming so. Laskey (1958:212) records one pair that remained mated for three years, did not migrate, and remained together winter and summer. In late February, I once observed two birds in company; one was feeding the other, as is characteristic of late phases of courtship. This occurred when little courtship of any kind had been seen in the area.

Among first-year birds, courtship activity is restricted, and many of these birds, at least those that are migratory, probably do not nest. Their reproductive states never advance beyond early courtship. The gonads of these birds are small but not so small as the gonads of Blue Jays in winter in this region.

Late Courtship in the Blue Jay

Courtship feeding.—As previously indicated, late courtship activities seem to evolve gradually from earlier courtship by flocks. The number of males in the flock is reduced to one, the latter seemingly eliminating his competitors by intimidation—aggressive behavior and fighting in some cases. The most characteristic activity of late courtship groups is feeding of the female by a male.

In rare instances I have observed the stage of courtship immediately preceding the final stage, and characterized by the presence of two males and one female in association. When three birds compose a courting group, two are in closer association with each other than is either with the third individual. One of these two regularly feeds the other, and the third is always a "bystander" (but obviously a member of the group). Thus, courtship feeding enters the courtship ritual before the group of jays is reduced to one male and one female. Courtship feeding in groups of three or two birds is the same.

The birds involved in late courtship usually feed calmly for as much as 20 minutes, showing no signs of courting. This low intensity of display persists in courtship feeding until the time of false nestbuilding. The only notes uttered, typically, in these periods are low conversational ones, *kut* or *kuet,* which are low intensity communication signals between the birds. These signals may be uttered softly in series, *kut kut kut,* when a bird flies or when it approaches its fellow with food. In feeding, the male approaches the female, which may accept the offering with hardly any display save for a slight crouching. Mildly intense forms of

FIG. 1.—A group of Blue Jays in courtship display. Uppermost bird is the female.

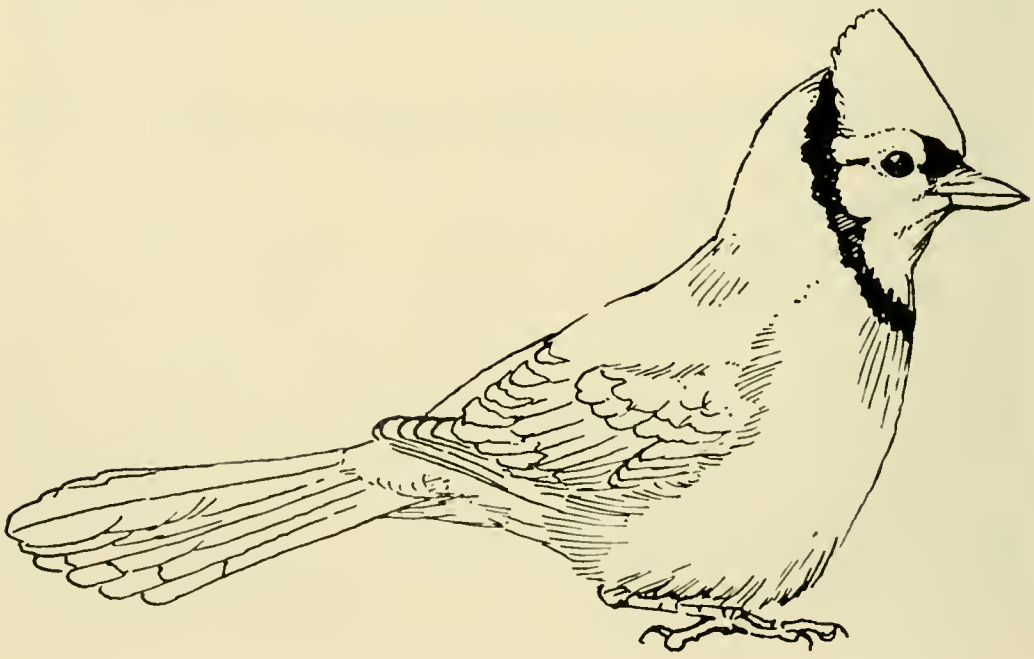


FIG. 2.—A Blue Jay in aggressive display toward a nonpredator.

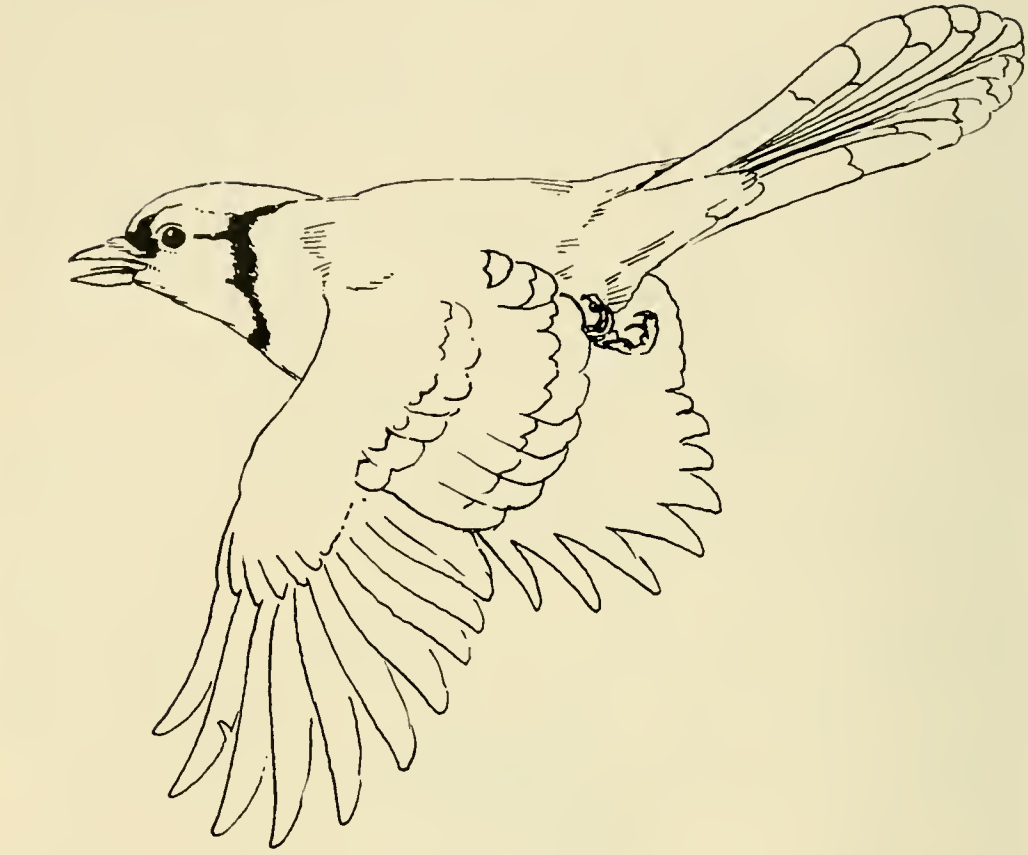
this ritual may involve on the part of the female slight flutterings of the wings and the uttering of the solicitation call—*kueu kueu kueukueukueu.* This call is given by the female, not only when begging for food, but also at the time of copulation. The call might better be termed a submission vocalization at these times, but it differs in being slightly more intense. The male may utter the same notes as he responds to the female's begging or submissive behavior. In the display, the female crouches (rarely does not crouch) with wings slightly drooped, tail and head tilted upward, crest lowered, and bill either slightly open or closed. At the height of this display, the posture changes slightly; the wings are quivered, and the tail is slightly spread (Fig. 5).

When there are only two birds involved in this form of courtship, it is obvious that they are male and female, and in most instances adult birds. In the instances where three birds are in company, the third participates only in a casual way, and I am not certain of its status. There has never been any indication that the third bird was another male competing for the female, or whether it was an adult or first-year bird. Perhaps the role of this bird is related to "helpers at the nest" to be discussed under the Mexican Jay.

The area of activity of these latter courting groups seems to be about the same size as that of the earlier flocks in courtship, although the birds may remain in one place for longer periods of time and seldom fly long distances. There is no anxiety and no chasing of the female; probably this results in the more casual, slower movements of the group.

The courtship activity of this phase of the breeding cycle is functional in that the ritual actually involves one bird feeding another bird, a habit that will be maintained through all the later phases of the cycle. In nestbuilding, the male will begin by presenting sticks to the female in precisely the same way he presents food; the female's begging behavior will be the same as before. In laying and incubation, the female will be the only one occupying the nest; the male will feed the female there. After the young hatch, they assume the begging role; both parents will present them with food. Thus, courtship feeding and begging rituals are intimately tied to functional reproductive behavior, sharing what seems to be the same motor patterns, and closely related stimuli and responses.

Whereas in the earlier phase of courtship, the groups of birds remain together for only a few hours in the mornings, the two or



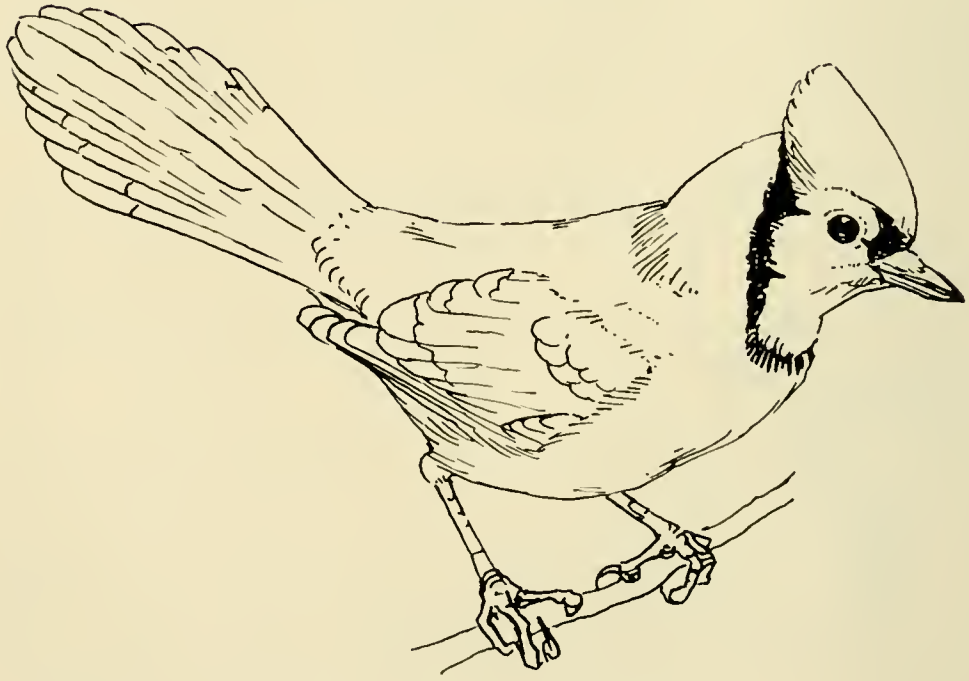


FIG. 3 (upper).—A Blue Jay in the Display Flight of courtship.
FIG. 4 (lower).—A Blue Jay in aggressive, investigatory posture toward a predator or strange object.

three birds associating in the phase of courtship feeding remain together constantly whether courting or not. Moreover, courtship feeding is not limited to any particular time of day, occurring with seemingly equal frequency throughout the daylight hours.

False nestbuilding.—The final stage in the courtship of Blue Jays involves a phenomenon heretofore seemingly unreported. This is the building of a false, or symbolic nest immediately prior to the building of the true nest, or sometimes contemporaneously with its early stages.

In eastern Kansas, this phase of courtship becomes evident in middle and late April. Like the forms of courtship previously discussed, false nestbuilding occurs mainly in early morning. If the activity is not observed closely over a period of several hours each day for several days, it might be mistaken for true nestbuilding. The habit has been exhibited by every pair of Blue Jays I was able to follow through to building of the true nest. False nestbuilding arises directly from courtship feeding, involving somewhat similar stimuli and motor responses, and subsequently evolves to nestbuilding, possessing similarities also to that habit.

Courtship feeding continues in false nestbuilding behavior, but the male, in addition to feeding the female, also gives sticks to his mate. These sticks in all cases are broken from trees, often near the false nest-site, but sometimes as much as 100 yards away. The sticks are never picked up from the ground. Often, food and twig presentation by the male are alternated, but at the height of intensity of the behavior, more twigs may be presented than food. The female crouches on the false nest-site; she may occasionally leave for brief intervals but always returns to it to accept food or a twig from the male. If the male is absent for more than a few minutes, the female utters a mewing cry not unlike that of the Catbird (*Dumetella carolinensis*) until her mate returns. This call may be correlated specifically with interruption of a sequence of events composing a courtship ritual at a time in the sequence when stimulation of the female is great; the call may, thus, be comparable to displacement motor responses expressed by animals frustrated in a tendency or drive. Whether the call serves to "summon" or "solicit" the mate is not certain. The female receives twigs and food while in the solicitation display posture (Fig. 5), with wings extended slightly and quivering. She utters begging notes, *kueu kueu,* during the presentation. Accepting twigs, the female makes an attempt to arrange them beneath her on the limb. If twigs are dropped in the

process of arrangement, the birds do not attempt to retrieve them. Sticks may accumulate at the false nest-site, but the accumulation never takes the shape or stability of a true nest. Moreover, a false nest never becomes the true nest of its builders, although it is sometimes used as a base for a true nest by another pair of jays.

Only once have I observed more than two birds seemingly involved in false nestbuilding at the same site. One of these three, attended and pursued by the other two, flew into the tree containing a small platform of sticks, went to this false nest and crouched on it. The other two jays remained nearby, and all three were silent. After three minutes one of the two bystanders flew away. Immediately afterwards, the crouched bird hopped up and began uttering the rattling *br'r'r'r'r'* call, at the same time bobbing vigorously. The bird (presumably the female) then began hopping upward through the tree, twisting from side to side, with crest raised. The remaining bird followed, duplicating the other's motion. Both were silent and soon departed. A week later only two birds were active at this same false nest. The involvement of three birds in false nestbuilding is probably rare, but its occasional occurrence is to be expected as a holdover from the feeding phase of courtship.

False nestbuilding leads to true nestbuilding, and for a day or so a pair may indulge in both activities alternately. In such instances the material for the true nest is gathered from the ground by both birds for a few minutes; the activity then switches to the false nest. As before, the female crouches at the site and the male brings sticks broken from trees.

Some exceptions to the general order of events in false nestbuilding may occur. Rarely, the female may be absent from the false nest-site when the male arrives with a stick. In such instances, the male may attempt to place the stick on the site and afterward may crouch there in the manner of the female. The male then may hop away when the female returns, but if he does not the female may go through the action of feeding the male or attempting to do so. The latter in such an instance does not solicit the presentation and exhibits no definite reaction of any kind to the offering by the female. It is generally thought that solicitation display by one bird stimulates another bird to make a presentation. The behavior described above indicates that in false nestbuilding either sex reacts positively to another bird crouched at the false nest-site by coming to that site and giving the presentation display. The latter display in turn is stimulus for a begging response by the female but elicits no positive

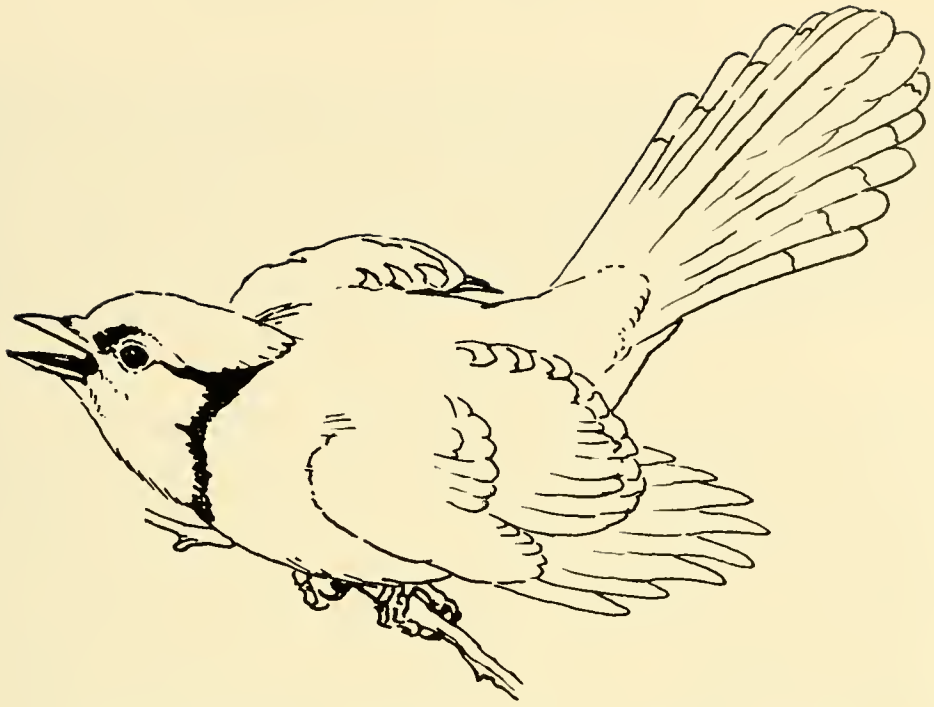


Fig. 5.—A female Blue Jay in the solicitation display of courtship feeding.

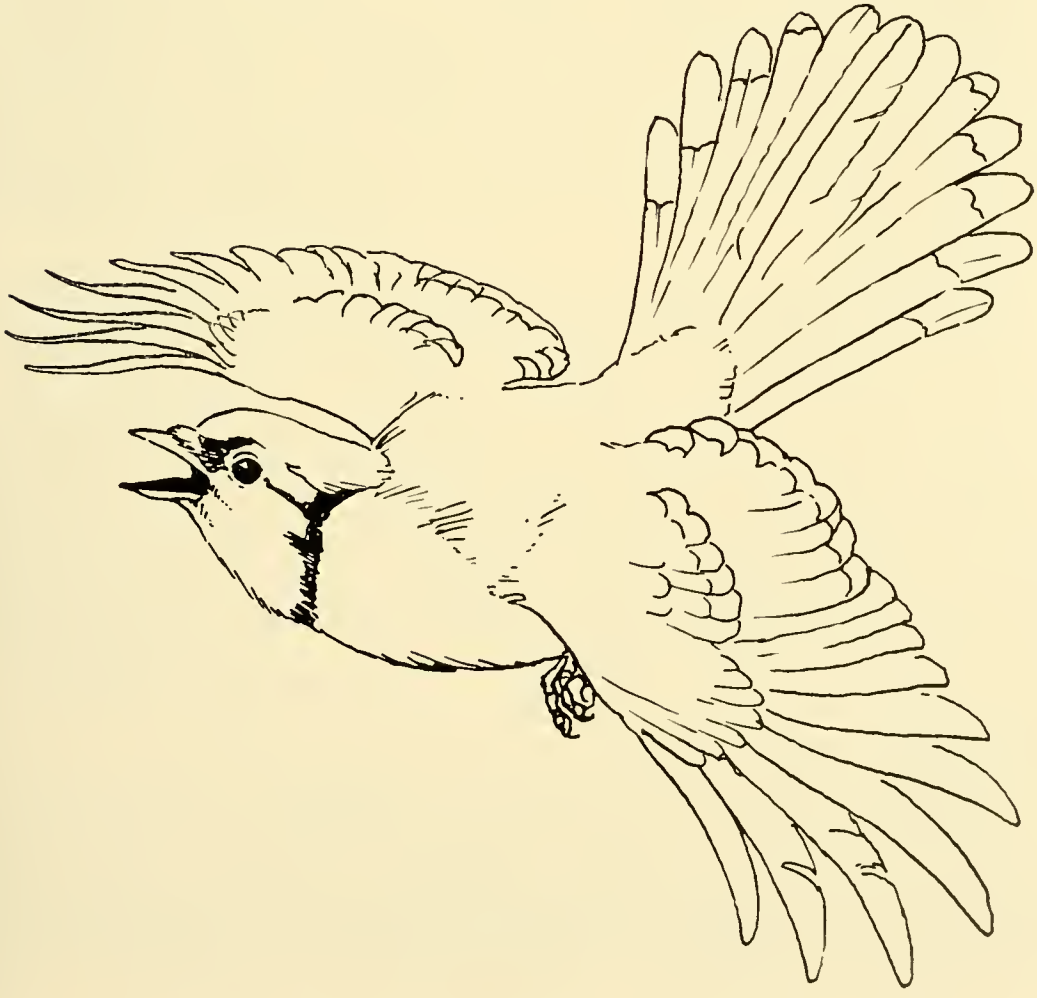


Fig. 6.—A female Blue Jay in the precopulatory display and copulatory posture—a submissive display.

response by the male. Only the male's failure to give solicitation display prevents courtship behavior from being reversed—all other positions and reactions of the two birds necessary for successful presentation and acceptance seem possible by both sexes. Either bird may occupy the stimulating position, either may react by flying to the crouched bird, and either may give a presentation display.

Courtship in the Mexican Jay

My observations of the prenesting habits of this species were made in a week spent in the Chiricahua Mountains in early April, 1958. In this period, I found Mexican Jays occupied with several phases of the breeding cycle. Some were not yet nesting, others were building nests, one pair had eggs, and another had young in the nest.

Prenesting flocks.—The majority of the birds were engaged in activities seemingly without counterparts in the other species here considered in detail. The birds moved about in flocks of four to 20 individuals, precisely as they do in summer. These flocks were not courtship groups like those in the Blue Jay; little display, posturing, or aggressive movements occurred among members of the flock, or were other activities of courtship discernible. Most of the flocks were small, having between four and eight birds. One of these may have been a family group; this flock consisted of approximately five birds, of which I was never able to find more than two, fully black-billed, adults.

In this species, a parti-colored bill is characteristic of most races (including *arizonae*) during a varying number of months or years before the black-billed condition is attained (Pitelka, 1951:317). Whether attainment of a black bill is exactly correlated with sexual maturation is not certain. Birds with parti-colored bills were neither members of pairs that constructed nests nor were they in any way intimately associated with nesting activities, as were the black-billed birds. The parti-color condition of the bill in two Mexican Jays that I kept in captivity from summer 1956, to spring 1958, did not change much in this time; the condition may not be correlated with sexual maturation. The testes of one of these captives measured 15 x 8 mm. on April 30, 1958.

Courtship feeding in the wild.—In the five days in early April, I did not observe one instance of courtship feeding in Mexican Jays. On only two occasions, did I observe any approach toward this behavior. A small flock of perhaps four birds was feeding along a road bank on the ground. One of these birds, perched in a low

tree, suddenly flew down near another jay on the ground and gave a low intensity begging display. In this display, it barely quivered its wings and extended its neck in an arched manner. The bill of the bird was not open, nor was any call given. It slowly circled the other jay, which simply turned to face the circling bird; no feeding occurred. The display lasted for less than five seconds, after which both birds flew off with the other two birds in the flock. Both birds involved in the display were adults, with fully black bills.

In the other instance of possible courtship feeding, a flock of 12 jays was moving about in a woodland, feeding quietly. When I approached, they grew excited, and six of them flew into the topmost dead limbs of a tree; for a few moments they perched quietly. At least eight, and possibly ten, of the entire flock's members possessed parti-colored bills. One of these individuals moved close to a black-billed bird, and their bills touched. It seemed that the bird with the parti-colored bill inserted its bill into the gape of the black-billed bird. No special posture was associated with this incident. The contact lasted for approximately two seconds. The bird with the parti-colored bill flapped its wings and jerked its body up and down during the contact. It is possible that this was aggressive or combative behavior, for Mexican Jays in captivity display a combative habit in which one bird grasps the bill or some other part of another bird. This habit is discussed under Social Order in captive Mexican Jays.

Gross (1949) does not seem to have observed courtship feeding in the wild in Mexican Jays prior to nestbuilding. He did see (1949:244) one feed another sitting on an uncompleted nest.

Courtship feeding in captivity.—Studies of captive Mexican Jays indicate that courtship feeding may be a habit as well-developed in this species as in other jays, regardless of my failure definitely to observe it in the wild. Mexican Jays placed in capitivity in July, 1956, and maintained in an outdoor cage at Lawrence from August, 1956, until May, 1958, first displayed courtship feeding behavior in April, 1957.

Of the captive Mexican Jays, three were males and one was a female. Two of the males were black-billed, but one had a considerable amount of white at the angle of the gape. The female had a slight trace of white on the bill. Figure 7 illustrates the heads of these four captives. It will be convenient to refer to the individual captives by letter symbols that were used to designate them in the study and referred to the color of the band or bands around

the tarsi of each bird. The fully adult birds were color-banded red on the right leg (RR), and white on the left leg (WL), respectively. The remaining birds were banded red on the left leg (RL), the female, and white on both legs (WW).

Rate of courtship feeding in captive Mexican Jays varies greatly and occurs mainly in the morning. At its greatest frequency, courtship feeding may average once every five minutes. It never occurs at such a rate for more than about one-half hour. Approximately one-half the time the bird receiving the food does not eat it immediately but stores it in a crevice. Afterward the bird returns to these caches and eats part of the stored food. Sometimes after eating the food immediately upon receiving it, the receiver goes to stored food and eats part of it too, but this is rare.

Feeding in each case is accomplished with little display. The recipient sometimes quivers its wings slightly and usually crouches in taking the food. The call given by the recipient, or, rarely, by the feeder, is *kwa kwa kwa*—a low intensity vocalization given with the bill closed. In a slightly more intense display, the *kwa* notes may be preceded by a short *ree*, hence, *ree kwa kwa kwa.* A conversational note may also be uttered in connection with feeding: *rook* or *ruk*, resembling the *kut* or *kuet* notes of Blue Jays. No display or special posture accompanies this note.

For a week after courtship feeding began in the captive birds, I saw feeding take place only between two of the four birds. The feeder in this ritual did not otherwise seem to be clearly the dominant one among the four birds, although at this time my information was limited. The recipient was at the bottom of the order, however. The two non-courting birds were unconcerned with the courtship taking place. One of these noncourting birds remained relatively solitary throughout its life in captivity. The other eventually assumed the position of feeder in the courtship ritual, to the exclusion of the previous feeder. This change in the right to feed in the courtship ritual was seemingly an expression of an exchange of positions of the two feeders in the social hierarchy and did not arise directly from competition between the two birds for this feeding right alone. When this change occurred, the ritual of courtship feeding gradually became more intense, involving greater vocalization and more definite display. However, less actual feeding seemed to take place in the ritual.

In courtship feeding, the recipient follows the feeder about wherever it goes. The recipient lowers its head near the feeder

as the latter picks up seeds. The recipient also pecks weakly at the bill of the feeder. This pecking at first elicits no response from the feeder but if continued for several seconds provokes a threat display (see discussion of sociality, p. 101) and, subsequently, a strong peck. The recipient may peck back but not vigorously. When the feeder is opening a seed, the recipient peers over the feeder's shoulder and then attempts to take the food. The feeder may then give a small particle to the recipient, but this never happens when the latter is vigorously attempting to take the food. The recipient may then attempt to return the food to the feeder, which seems never to accept it. After this display, the recipient usually stores or eats the food in a normal manner.

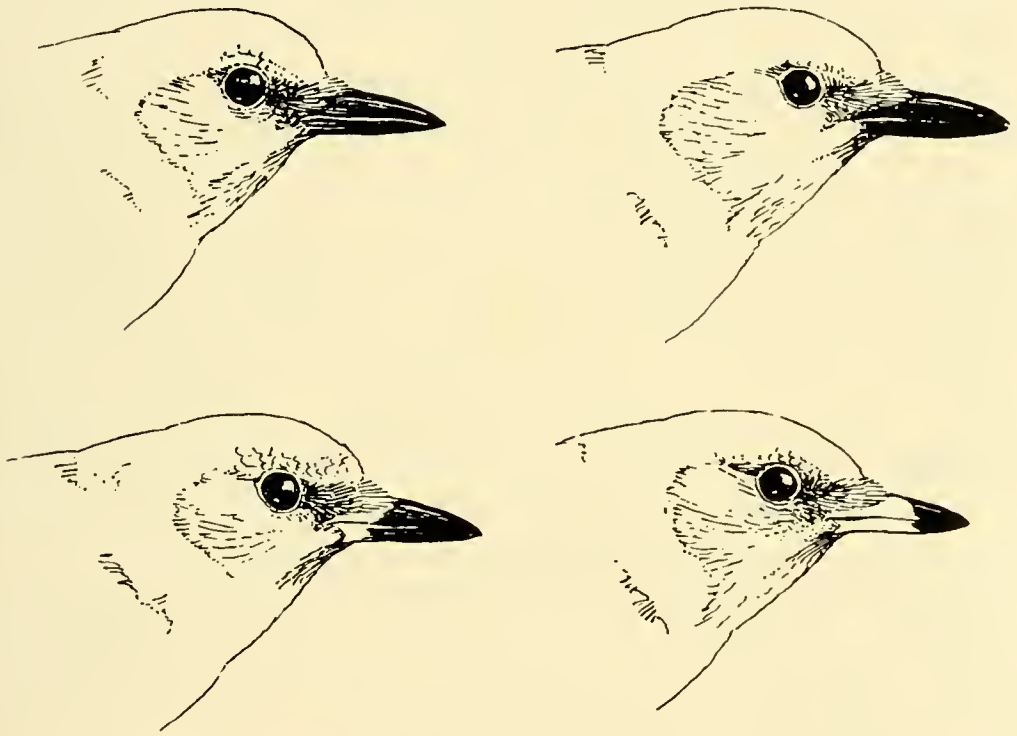


FIG. 7.—Heads of captive Mexican Jays. The parti-colored bill is evident in two of these birds. Upper left, WL, male; upper right, RR, male; lower left, RL, female; lower right, WW, male.

Courtship feeding declines in frequency approximately the first week after its initiation but continues sparingly through most of the spring.

The significance of courtship feeding and its relationship to social order.—Mexican Jays with parti-colored bills engage in courtship feeding activity, a fact that indicates some first-year birds may reach breeding condition in the wild. It will be recalled, however, that Blue Jays engaged in courtship activities in May and

June are first-year birds and are probably nonbreeding individuals with only slightly enlarged gonads. I have mentioned previously (p. 30) that the testes of one of the captive Mexican Jays with parti-colored bill reached a size indicative of breeding condition (15 x 8 mm.).

In the captive Mexican Jays, a female (RL) habitually fed a male (WW), reversing the usual relationship in courtship feeding of wild corvids. Such reversal indicates that the factors initiating the behavior are more complex than the term "courtship feeding" can indicate.

In such a highly social form as the Mexican Jay of Arizona, the necessarily frequent interactions of individuals seemingly require the establishment of a social hierarchy if the birds are to remain together in a peaceful flock. Thus, in interaction of two individuals, the quick establishment of one as dominant, the other as subordinate is important. The basis of dominance of one bird to another is superior strength; that is, in the initial competitive interaction between two individuals, superior strength in fighting establishes the victor as dominant over his opponent. But in the interests of conservation of energy, preservation of individuals other than dominants as members of the breeding population, and to a certain extent the facilitation of relatively peaceful (noncombative) survival of the social group, fighting is impractical. It has been superseded by ritualized postures and aggressive movements involving brief contact or none and accomplishing the same purposes as fighting following the initial interaction.

Unnatural conditions created by captivity may have been enough to alter the behavior of captives. Yet, the appearance only in captive birds of reversed "courtship feeding" does not reduce the significance of this unnatural behavior.

Courtship feeding, which occurs only in the breeding season, may be an expression of dominance of a male to a female, although it is not a method of maintaining dominance. Of course, in order for courtship feeding to be considered an expression of dominance in wild birds, it must be assumed that males dominate females at this time of year in all activities. Observations bear out this supposition. There are two categories of self-sufficient individuals of the Mexican Jay—adults (black-billed) and younger birds (parti-colored bill, exclusive of juveniles and nestlings). In the social order of captive birds, black-billed birds dominate birds having parti-colored bills. Birds with a small amount of

white on the bill dominate individuals having a large amount of white on the bill. In a given population, amount of white on the bill (degree of parti-coloredness) may be considered a general index of age. Thus, age influences social order, older birds dominating younger birds.

Since the captive bird fed by two others was also dominated by them, domination and feeding may be correlated and are possibly related expressions of the same attitudes, the feeding action being an expression of dominance modified by sexual tendency. In my captive Mexican Jays, the youngest male was fed by two other birds, one an older female (a slight trace of white on the bill), and the other a fully adult male. It seems unlikely that the two older captives were reacting toward the young male in the role of parent, since the latter was at least nearly a year old. Age, then, seems to be more important than sex in determining social order and determines dominance when the two factors conflict. It may be further concluded that old females do not feed younger males in the courting manner in the wild because conflict between the factors of sex and age are reduced. Reduction of this conflict may be correlated with lack of confinement and the presence in the flocks of aggressive, adult males; both factors might discourage adult females from feeding young males.

Nestbuilding in courtship.—In the Mexican Jay, nestbuilding seems to be an integral part of courtship, and may be more comparable to false nestbuilding of the Blue Jay.

Scott (1886:82) was perhaps the first to publish evidence of the epigamic nature of nestbuilding in this species, although he did not recognize it as part of courtship. Scott discovered these jays mating in late February and found a completed nest on March 16. No eggs were deposited in this nest until April 1. In the period from March 16 to April 1, an adult frequently sat on the nest and also built another nest within a few feet of the first one.

Gross (1949:242-6) gives an excellent account of nestbuilding by Mexican Jays; his observations differ slightly from my own. He describes how all the members of a flock visit the nest-site periodically, with one or two of them carrying sticks for the nest. No more than two birds at a time brought material to the nest-site, but other members of the flock stood close by and occasionally flew down to arrange the nest material others had placed there. The visits of the flock to the nest were made as often as five times per hour. The birds made no pretense at secretiveness around the nest,

all coming with loud calls and perching around the nest while material was added. The flock included both black-billed and parti-color billed birds, although the latter were not seen to help build the nest. The main body of the nest was composed of sticks broken from trees and was lined with rootlets and horsehair. Finally, Gross noted that false nests were built by the flock, and that even the true nests were often completed long before eggs were laid in them. One flock spent nine days building a false nest and then constructed the true nest fifty feet from it. In another instance, a nest was seemingly completed thirteen days before the first egg was laid, although a jay was occasionally seen sitting on this nest in the interim.

In the Chiricahua Mountains, I discovered two completed or nearly completed nests on April 1 and 2 and made daily observations of them through the morning of April 6. No eggs were present in either of these nests, and there were times when I was, erroneously, almost convinced that these nests were inactive. A flock of approximately a dozen birds moved about throughout the day in the vicinity of each nest. The activities of the birds were mainly social, not having to do with breeding. Yet, in the morning hours the flock would move near the nest several times, sitting in and around the tree containing the nest. At these times, two adult birds would leave the flock and go to the nest-site. Typically, the others maintained a distance of ten to 50 feet. One of the two adults then sat on the nest and moved about as if molding the cavity of the nest; the other bird perched close by. On one occasion, the sitting bird left the nest and returned with fine grasses (this activity was also observed at another nest). The other adult usually did not sit on the nest, but examined it closely, sometimes perched on its rim, and occasionally settled tentatively on it. The birds sometimes pulled at twigs near the nest, as if trying to add these to it. These twigs were never added to the nest, although I noted, as did Gross (1949:243), that most of the twigs comprising the nest seemed to have been broken from trees by the birds. The bird that most often sat on the nest usually remained on it for less than five minutes, but sometimes remained for as long as 10 minutes.

The birds showed little concern for my presence, and in fact they were noisy in the vicinity of the nest at all times. Vocalizations included assembly calls, *reek reek* or *ruik reek ruik reek.*

I found no definite evidence of false nestbuilding in this species as did Gross (1949:242-6), although one flock of jays under observation were active periodically in two adjacent trees each of

which contained a partially constructed nest. The birds actually visited only one of these two nests, however; the other may have been a false nest of this flock of jays, since it did not seem to be an old nest from the previous year.

In one of the above flocks, most of the birds were adults. The other contained only two black-billed birds (those that came to the nest). From the latter flock I shot a member possessing a parti-colored bill. It was a female with ovary slightly enlarged. Adults collected at other nests on the same day showed enlarged gonads. Flocking at the time of nestbuilding, and the fact that the nest-building birds are active members of these flocks are indicative of the strong social bonds in the species. These bonds remain strong throughout the remainder of the breeding cycle; members of the nesting pair participate in care of the young.

Variation in flocks.—The flocks associated with nests vary in structure. Of three such groups under observation in April, one consisted of six black-billed birds. Two nests of this flock were located within 150 feet of each other in a grove of oaks in a gully on a hillside. On April 5, one nest contained four eggs, the other contained young birds about a week and a half old. In two hours of observation near these nests, I found only two black-billed birds in the vicinity of each. I collected the birds at the nest containing four eggs, and still no other birds appeared there.

A second flock consisted of approximately a dozen birds; four or five were black-billed. Only one nest was found in the area of this group. The nest was still under construction. The third flock consisted of about eight birds, two of which were black-billed. These birds were associated with the only active nest found in their area.

It may be significant that the flock consisting wholly of black-billed birds was much farther along in the breeding cycle than the other two flocks, members of which had parti-colored bills. In most other species of passerine birds, adults begin the breeding cycle before the younger birds; thus, it is reasonable to expect a considerable shortening of the time of preliminary activities of breeding—activities such as pair formation and courtship—in flocks composed of adult jays, resulting in relatively earlier breeding. This, of course, is tenable only if birds with parti-colored bills are sexually immature or later to mature. It is possible that a flock might become composed entirely of old birds through loss of subadult members, failure to have a successful nesting season several years in a row, or other chance factors.

Comparison of Courtship Habits and Pair-bonds

The differences in the patterns of courtship of jays under consideration in this paper seem to be direct expressions of the differences in sociality of the several species. The Mexican Jay remains in a highly social flock throughout the period of courtship. If there is at this time competitive, aggressive display between males, it is certainly not common; the flock as a whole does not engage in specific displays and aggression. Within these social flocks some method of pair-formation exists; courtship feeding occurs, and periodic ritualized behavior connected with nestbuilding is unquestionably important as a late phase of courtship. But the flock's social bonds are strong; the pair remains in the flock. Or, perhaps better, the flock remains with the pair, being influenced so much by the reproductive behavior of the nesting birds that it forms a social "circle" around them. In any event, the epigamic gestalt of the Mexican Jay is a primary result of the prominent social disposition of the species; whether such sociality facilitates or stimulates breeding behavior, as Richard F. Johnston (verbal communication) has suggested, is not known. Pairs in fact carry out breeding activities without attention from other individuals, but it seems likely that reproductive success is greater when the pairs are members of flocks because of the frequency of the habit.

Blue Jays cease to flock midway through courtship in most cases. Flocks of Blue Jays in spring may be termed epigamic flocks; they are concerned almost solely with early courtship. In the late phases of courtship of the Blue Jay, false nestbuilding occurs, but this happens after complete dissociation of the pair from other members of the flock. Behavior in the Mexican Jay involves building of true and false nests while the pair retains full membership in the flock and utilization of the true nest as well as the false nest in the courtship ritual. I have recorded only one instance of there being more than two Blue Jays in association during false nestbuilding. In this instance three birds came to the tree containing a false nest and one went to the structure and sat on it. Thus, although this stage of courtship in the Blue Jay is rarely reached until all but one male and one female are eliminated from active roles, there seems to be a tendency for "extra" birds to be inquisitive about, or to associate, however loosely, in late, intimate phases of courtship.

It seems likely, as indicated previously, that there is survival value inherent in the presence of a group of nonbreeding birds living with and assisting the breeding pair in the Mexican Jay.

In one pair of Blue Jays observed in this study, the male disappeared in early incubation and the female acquired a new mate before the young were hatched; the nesting then was successfully completed. The second male associated with this nest was a first-year bird. This may indicate that there are nonbreeding males interested in or at least aware of nests in their foraging areas; these non-breeding birds do not appear at the nest where both members of the pair are active but appear when the male is lost. That the acquisition of the new mate by the above female Blue Jay had survival value is probable. There may well be a common basis for such an acquisition and the phenomenon of helpers at the nest, indicating a degree of relationship between Blue Jays and Mexican Jays.

Acquisition of a new mate after nesting has begun is seemingly rare, in passerines at least, but there is ample precedent for this phenomenon in corvids. Shannon (1958:401-2) mentions seven published accounts of late replacement of mates (all females it should be noted) in the Magpie (*Pica pica*); replacement may occur in that species after the young are hatched, and a new mate may be acquired within seven hours of the loss of the first one. Thus, although there is a diverse social phenomenon surrounding the pair-bond in different corvids, there seems to be an especial, possibly adaptive, flexibility in the relationships of adults and first-year birds, males and females, common at least to Mexican and Blue Jays and Magpies, among New World garrulines.

Displays and postures associated with courtship behavior in the Blue Jay show greater ritualization, specialization, and intensity compared with homologous patterns observed by me in the Mexican Jay. Similarly, the variety and complexity of calls is greater in Blue Jays than in Mexican Jays. In short, the complexity of behavior concerning pair formation and maintenance seems to vary inversely with degree of sociality of the two species.

The Scrub Jay is the least social of the forms under discussion. Consequently, the dissociation of members of flocks occurs earlier in the breeding cycle, and although my information is limited, it seems that the process of courtship and pair-formation in the species is even less associated with activities of the flock than is true in the Blue Jay. In late March and early April in the Sandia Mountains of New Mexico, the weakly formed winter flocks of Scrub Jays have completely dissociated, nestbuilding has begun, and courtship feeding is a frequent activity of the pairs.

The Scrub Jay in Florida, *Aphelocoma c. coerulescens,* is an exception socially among races of the species for which breeding habits are known. Therefore, information concerning epigamic behavior in that race may not be applicable to the species as a whole. Nonetheless, this is the only race of the Scrub Jay concerning which I have found a statement about courtship. Bent (1946: 79) states that S. A. Grimes of Jacksonville, Florida, is of the opinion that in the Florida race the birds remain paired throughout the year. Bent concludes from this and the lack of other observations of courtship in Scrub Jays that courtship does not occur in the species. It may instead be an indication, I think, that courtship does not involve highly overt, complex behavior, as in the Blue Jay. Either explanation is tentative; Bent (1946:34) as a matter of fact concludes ". . . that courtship is not a conspicuous feature . . ." of the Blue Jay's behavior because "A survey of the literature brings little to light . . ." concerning courtship in the species. Nevertheless, Bent does continue by documenting several examples of courtship in the Blue Jay.

NESTING ACTIVITIES

Nestbuilding in the Blue Jay

Both the male and female Blue Jay usually participate in building the nest. In some pairs, both male and female participate about equally in bringing material to the nest, but in others the female does most or all of the work, the male following her about, occasionally picking up a piece of string, large stick, or brightly colored piece of paper. The male's effective contribution to construction of the nest may thus be negligible; he may carry fully as much material to the nest-site as does the female or at least make as many visits to the nest. But the male is usually awkward at nestbuilding, and frequently the material that he transports is eventually dropped to the ground, unless the female is present to prevent this. Nestbuilding occurs primarily in the morning hours, and, as mentioned previously, may be alternated with false nestbuilding activity.

I have never seen more than two birds building a single nest. Thus, it seems probable that normally the last remnants of groups with three or more members disappear with the commencement of activities in breeding of a non-courtship nature. Maintenance of the pair-bond, to be sure, involves the same behavioral patterns that are present in courtship: Feeding of the female by the male continues,

strange jays are chased away by the male, and the members of the pair remain together almost constantly.

In the construction of one nest in spring, 1957, the male assisted little; while the female gathered nest material, he usually perched in a conspicuous position nearby. It seemed that the male served as a "lookout" for danger to his mate. The male's function as lookout seems to be more prevalent in the Scrub Jay, under which I have described the habit more thoroughly. I might have overlooked this habit in the Blue Jay in which it occurs uncommonly had it not been for my observations of it as a functional pattern in the Scrub Jay.

Material for the nest is gathered by Blue Jays over a wide area around the nest-site. This area probably corresponds to the home range of a pair. I watched one pair build a nest, for which much of the material was gathered approximately one quarter mile from the site. The nest was located in a tall pine surrounded for some distance by a lawn relatively clear of dead grasses, sticks, paper, and other items commonly used in building nests. When such materials are available close by, the jays seldom fly farther to secure them.

Blue Jays will use paper, or other more unusual materials for nest construction; with an ample supply of some item such as crepe paper available, a great part of the nest may be constructed of it. I knew of one nest in a tree near a picnic ground that was visible from a considerable distance because its base was composed largely of pieces of paper napkins.

Several behavioral rituals are connected with nest-building, although none are confined to that phase of the breeding cycle. They include the solicitation display by the female near or at the nest, feeding of the female by the male, and presentation of nest material to the female by the male. The last of these is rare, the male usually placing the nest material directly on the nest. The birds are relatively quiet while building and remain less vocal through the remainder of the breeding cycle until the young leave the nest. Calls most frequently uttered are those associated with the above rituals—*kueu kueu kueu* and the conversational notes, *kut* or *kuet*. Other calls may be given, but only when the nestbuilding activities are interrupted by activities completely apart from breeding behavior.

Nestbuilding seems never to take more than five days. Usually by the second day of construction, the nest has attained considerable

form. It is on the second or third day that the most intense activity in construction takes place. Through the first day and part of the second, time is frequently divided between the false and true nests. By the third day, only occasional visits, if any, are made to the false nest-site.

In one pair observed in the first day of nest construction, each bird brought material to the nest eight times in 60 minutes; the female's efforts contributed the most. The birds worked closely together, on two occasions coming to the nest at the same time with material from the same place. At the beginning of this hour, they made visits to the false nest, where the female perched quietly. The male fed her there on two occasions, but never did so at the true nest during its construction.

At another nest on the second day of construction, the female brought material 11 times, the male eight times, in 60 minutes. The male was, again, somewhat less efficient in his work. Both birds frequently sat on the nest after bringing sticks, shaping the cavity with their breasts. The male several times deposited materials beside the female while she was on the nest. Twice he fed her at the nest and once away from the nest. Construction by this pair was begun on April 26 (the last day that false nestbuilding by the two jays was observed) and was completed on April 29, when the birds were bringing fine rootlets and fibers to the nest in the morning. The female followed her visits to the nests with periods of sitting on it, once for seven minutes. Later that day she sat on the nest frequently, and no further nestbuilding activities were observed.

The contribution to nestbuilding by members of a pair does not seem to vary much from day to day. That is, if the male contributes to nestbuilding the first day by visiting the nest with material 40 percent as often as does the female, he will do so in about the same proportion on the following days.

Nestbuilding and Associated Behavior in the Scrub Jay

I observed nestbuilding by a pair of Scrub Jays in the Sandia Mountains of central New Mexico in April, 1956. The activity was interspersed with courtship feeding, territorial displays, and other activities.

Division of duties and the "Sentry-Habit."—I discovered the nest (N-1; see figs. 8 and 13) when it was roughly half completed. An alternation of duties was being practiced by the pair. Both birds remained together constantly. One would go to the ground to

secure material such as grasses and sticks. Meanwhile, its mate stationed itself as a "sentry" in a prominent position (Fig. 9), usually the top of a juniper tree, nearby. Occasionally the sentry deserted its post for a few minutes at a time, but always returned in time to accompany its mate to the nest. Sometimes the sentry "anticipated" the flight of its mate to the nest and arrived there first. While its mate arranged the new materials in the nest, the sentry remained close by and not necessarily in a prominent position. Once the material had been incorporated into the nest, the bird standing by flew to the ground and gathered material while the other assumed a perch high above. Only occasionally the same bird gathered material twice in succession. When the birds flew a distance of more than a few hundred yards for material, both gathered some before either returned to the nest.

The sentry is so termed here because it seemingly serves as a look-out for possible danger while its mate is occupied in gathering nesting material. On one occasion when a Red-tailed Hawk (*Buteo jamaicensis*) soared over a sentry, it set up a cry of *kwesh kwesh kwesh kwesh*, flew quickly to its mate on the ground, and with her flitted off through the undergrowth. A bird standing on the ground, in this open, oak-juniper scrub and concentrating on gathering nest material or food is more vulnerable to predation than a bird undertaking the same activity in a woodland with a heavy canopy of branches and leaves overhead. The survival-value of the presence of a sentry seems definite.

From the hillside where I was making observations, I found that I could locate other territories of jays by the presence of sentries. The sentry-habit is not confined to the nestbuilding period; a bird gathering food in a conspicuous place may also be accompanied by a sentry.

The *kwesh* call mentioned above is one of the most frequent given by this species of jay. The call is usually uttered in flight, and, as with the *jayer* call of the Blue Jay, it is a low-intensity alarm call that alerts other jays but does not cause them to assemble.

Courtship feeding is interspersed with nestbuilding. A bird may fly up to its mate and in spite of holding grasses in its bill, seem to feed the other bird, after which the nest material is carried to the nest. In courtship feeding observed in the nestbuilding phase, there is notably little display by either member of a pair. The feeding is accomplished quickly, with slight or no fluttering of the wings by the female. Usually no vocalizations are given, but occasionally a suppressed begging call is uttered by both birds or by

the female. This call, *greer greer,* is given with the bill closed and is similar in sound and function to the *kueu kueu* call of the Blue Jay.

Associated with nestbuilding, and probably other phases of the life cycle, are two other characteristics that have counterparts in the Blue Jay. These are the rattling *br'r'r'r'r'* call and the *bobbing* display. The call is indistinguishable from that of the Blue Jay but is given much more frequently, although often in similar situations of seeming anxiety. It seems more easily elicited from the Scrub Jay. I have heard it after courtship feeding, and when the birds are alarmed by a human too near the nest. It is often associated with *bobbing,* which, as in one type of *bobbing* of the Blue Jay, seems to be an intention movement of flight. In fact, in the present species, I have not seen it used in association with courtship. (In the Blue Jay, when it is used in courtship it is accentuated to the point that the bird may actually leave the perch in the activity. It seems in other words to be ritualized and exaggerated in intraspecific intimidation.) The *bobbing* that I observed in the Scrub Jay resembles, then, the flight-intention movement of the Blue Jay, not the *bobbing* of that species in courtship.

Flight and flight-display.—The Scrub Jay of the subspecies *woodhouseii* is short-winged in comparison to the other species of jays herein discussed. Its flight is thus more labored than that of Mexican, Blue, and Steller's jays. Immediately upon launching into the air, *woodhouseii* resembles in flight the thrashers (*Toxostoma*), the path of flight being up and down, the tail flitting from side to side. In the launching phase, a peculiar sound is made by the wings, resembling the sound made by the wings of a Mourning Dove (*Zenaidura macroura*) in flight, but somewhat lower in frequency. If the jay flies a long distance, it eventually moves more easily; it may alternately glide and flap its wings. Flight caused by a human that is too close to the bird is a jerky, "thrasher-like" movement for short distances from perch to perch, where *bobbing* and the *br'r'r'r'r'* call are given. This intermittent flight may be a kind of display, although it is not at all like flight display of the Blue Jay.

The weak flight of this jay, at least in the launching phase or on short flights, may be another reason for the assumption by the bird of a prominent, usually high, perch when remaining at rest for more than a few seconds. The high position affords the bird an easy, swift take-off, albeit it downward at an angle into the undergrowth.

Territoriality

Territoriality in the Blue Jay.—Territoriality is exhibited by the Blue Jay for the first time in the nestbuilding phase of the breeding cycle. Although this phenomenon is not strongly expressed in the Blue Jay, it is nevertheless true territoriality. Its expression is

FIG. 8.—Tree containing nest of a pair of Scrub Jays (N-1) in the Sandia Mountains, New Mexico.

FIG. 9.—An adult Scrub Jay acting as a "Sentry" while its mate gathers nest material from the ground.

strongest from the time of nestbuilding until the young leave the nest, but territory is not defended at any time against other jays not in the same general phase of the breeding cycle as the resident pair. Thus, jays incubating eggs or feeding young in the nest will allow another pair with their young out of the nest to wander into the territory—even into the nest tree—in the course of care for these flying young.

A strange jay entering a territory may be greeted by one of the resident birds. The resident flies to the interloper and alights nearby. If the strange bird does not flee, it may give an erect display. If the bird is on the ground, the head is raised and held rigidly still, with bill forward toward the resident individual. The belly feathers are fluffed, the body held low, the back swayed, the tail held low and slightly spread, and the crest fully erected (Fig. 2). At the same time, the resident bird of the territory assumes a crouched position with head lowered and begins to hop cautiously in a circle around the interloper. As the resident circles, he makes threatening jabs with his beak at the strange bird, who turns to face the threatening bird as it moves. Such display may then be followed by a brief flurry of combat in which the birds fly at one another. Previous to combat, however, it is clear that the resident is the aggressive, dominant bird, while the interloper is the reticent, subordinate individual. Audubon (1834:12) noted in captive Blue Jays that when a strange jay was introduced into the company of others it fled to a corner and assumed an erect posture; moreover, a stiff, head-up posture is characteristic of subordinate Mexican Jays in interaction with dominant individuals.

In the European Jays (*Garrulus glandarius* and *G. lanceolatus*) the appeasement display of a subordinate toward a dominant individual is characterized by the body being held low, plumage fluffed, and head up as in the interloping Blue Jay mentioned above. But, in *Garrulus* the bill is pointed upward, not toward the opponent as in the Blue Jay, according to Goodwin (1952:304-6). The same author describes the display of aggression in *Garrulus:* it is a "lateral display" (bird turned at right angles to his adversary, crest raised, head held up with bill directed forward, feathers fluffed, and the body slightly crouched on the tarsi).

Erect (head-up) postures with bill directed forward or down often are indicative of intense threatening attitude, although threat postures are not all erect postures (see discussion of gulls by Tinbergen, 1955:119-25). Appeasement displays according to Moyni-

han (1955:252) are of hostile motivation just as are threat displays, but in appeasement the escape tendency is stronger than in threat. Though both types of behavior may deter attack from the opponent, the appeasement display does so by reducing the strength of the opponent's attack drive while not provoking a fleeing or escape tendency. Posture in appeasement seems to resemble that of threat in many cases but characteristically differs in that the bill and head are turned away from the opponent, either upward or backward.

The head-up display of the Blue Jay seems to combine elements of both threat and appeasement postures as described for other species. While the posture in the Blue Jay probably is basically a threat posture (the crest is raised, bill directed forward) it seems to have become ritualized as appeasement posture (the bird never attacks from this position, may actually avoid attack, does not employ the posture within its own territory, and never elicits an escape response from the opponent). The head is never turned away from the opponent by Blue and Mexican Jays in appeasement or other displays whereas such head turning seems to be a prevalent part of appeasement in *Garrulus* and many other birds.

Bobbing is occasionally employed in territorial encounters, especially those that occur above ground. If the resident male is foraging away from the nest-tree and a stranger alights there, the male returns, alights near the interloper, gives the *cleeop cleeop* call, and bobs deeply. If the trespasser does not flee at this intimidation display, the resident male may fly at the bird; a brief skirmish in which there is generally no body contact often ensues. In such encounters, the birds flutter toward each other and just before colliding mount straight upward, flapping their wings at each other like game cocks. The resident male sometimes fails to drive the stranger out of the territory. When this happens, the male ignores the stranger, which resumes feeding nearby as if nothing has happened. Blue Jays are often unsuccessful and show little persistence in their territorial actions. A jay driven from the territory sometimes returns again and is allowed to stay and forage.

Usually it is the male that engages in territorial struggles. The behavior of the female varies. She often remains on the nest but sometimes takes an active part in territorial skirmishes, especially if the male is absent when the trespasser appears.

Figure 10 is a map of a portion of an open woodland on the campus of the University of Kansas, showing the locations of nests

of Blue Jays in 1957. Also included are the locations of false nests of certain pairs, and the places where nest-material was gathered. The home ranges of most of these pairs broadly overlapped, the banks of the small lake being frequented by birds of N-1, N-5, and N-8 commonly and by birds of other pairs and nonbreeding individuals occasionally. Similarly the recreation area, used by humans for picnics, was common ground for all the jays in the vicinity—not just the pairs in the area under study. I did not observe territorial defense by all pairs, and I am certain that for some of these pairs such defense was infrequent. The pairs of N-2 and N-5 and pairs that had nested in this grove just north of the lake in previous years seemed to have the most territorial squabbles, principally because they often attempted to keep other jays away from a hedgerow along the north bank of the lake. They also seemed to have frequent encounters with birds halfway between their nests and Oread Hall. These encounters were in most instances with birds from nests in the N-3 area, which often flew down the hill into the grove of small oak trees there, to feed. I never saw territorial encounters at the recreational area; N-8 on the map (Fig. 10) represents the closest active nest to that area that I ever found. This is perhaps indicative of the attitude of the jays toward that place, which as previously stated was common ground for many jays.

The size of the Blue Jay territory is difficult, if not impossible, to ascertain, because of the irregularity of defense (both in time and place) of the area by the resident pair. I have never seen territorial defense more than 200 feet from the nest, although defense that distance from the nest was as vigorous as that undertaken nearer. Territorial boundaries seem to be determined more often by some distance from the nest rather than by the presence of obvious demarcations in vegetation or physiography. One pair defended several times along a "line" that must have been based upon distance from the nest. Vegetation and physiographic characteristics were uniform from the nest considerably beyond the maximum distance at which territoriality was exhibited.

According to Hinde (1956:343) there are often three main components of behavior in the establishment and maintenance of a territory. These are: (*a*) Restriction of some or all types of behavior to a more or less clearly defined area; (*b*) defense of that area; (*c*) self-advertisement within the area. Blue Jays exhibit all of these components in their behavior. In formulating a concept of territoriality in Blue Jays the following characteristics of the expres-

sion of the phenomenon in the species should be noted. Both males and females engage in defense of territory; territorial boundaries are not rigidly defined as in such classically territorial species as the Song Sparrow (*Melospiza melodia*); the adults feed and rest within the territory, only occasionally leaving it to visit some special food supply or to bathe; territorial defense is displayed neither regularly nor persistently.

Irregular defense of the territory seems to be based on the "attitude" of the interlopers. A jay that flies into the area, lands high in a tree, feeds young out of the nest, or behaves as a member of a courtship flock, will not be bothered by the resident birds. However, one that flies into the territory and begins at once to forage on the ground or in the low branches of trees, or uses the area as a resting and preening site, arouses territorial behavior in the resident birds. The interloper must behave as if he or she "belonged" in this area, before attack by the resident birds is instigated. This explains the irregularity of territorial display against strange jays. But it does not account for the lack of persistence in territorial behavior in the face of certain responses of the intruder, as mentioned earlier. Territorial display occurs so infrequently in Blue Jays that it is studied with difficulty. Therefore, the frequency of success of resident birds in territorial skirmishes is not satisfactorily computable.

Territoriality, in Blue Jays, involves maintenance of the pair-bond (but not pair formation), defense of the nest-site, and reduction of interference in reproductive activities by other members of the species.

"Territoriality" in the Mexican Jay.—Territoriality of pairs does not exist in Mexican Jays. The nesting pair may freely allow from one to five individuals—members of the flock—about the nest and young. Home range of flocks are separate with no overlapping during the time of breeding activity. Although I have never observed any behavior of the species that might be termed territorial aggression, the distinctness of the ranges of breeding flocks implies the presence of a spacing mechanism that is the effective equivalent of territoriality. We can only speculate as to the nature of this mechanism. In nonbreeding activity, two flocks previously distinct while breeding typically unite; the smaller, breeding flocks otherwise remain discrete. Thus, the spacing mechanism is probably involved with reproductive factors.

Perhaps the areas occupied by flocks have been maintained over

many generations; the flocks are relatively sedentary, the habitat nearly unchanging over the years. The change in individual composition of the flocks by old birds dying off, young birds taking their place is gradual. The young birds each year learn the boundaries of the home range by following their parents and associated adults of the flock. The boundaries have themselves been established so that sufficient food, shelter, roosting places, water, and other necessities are present to allow the existence of the flock, which remains fairly constant in size. If the foregoing is a satisfactory explanation of the spacing mechanism, then seeing the phenomenon at work in a short period of observation in the field is not possible; spacing

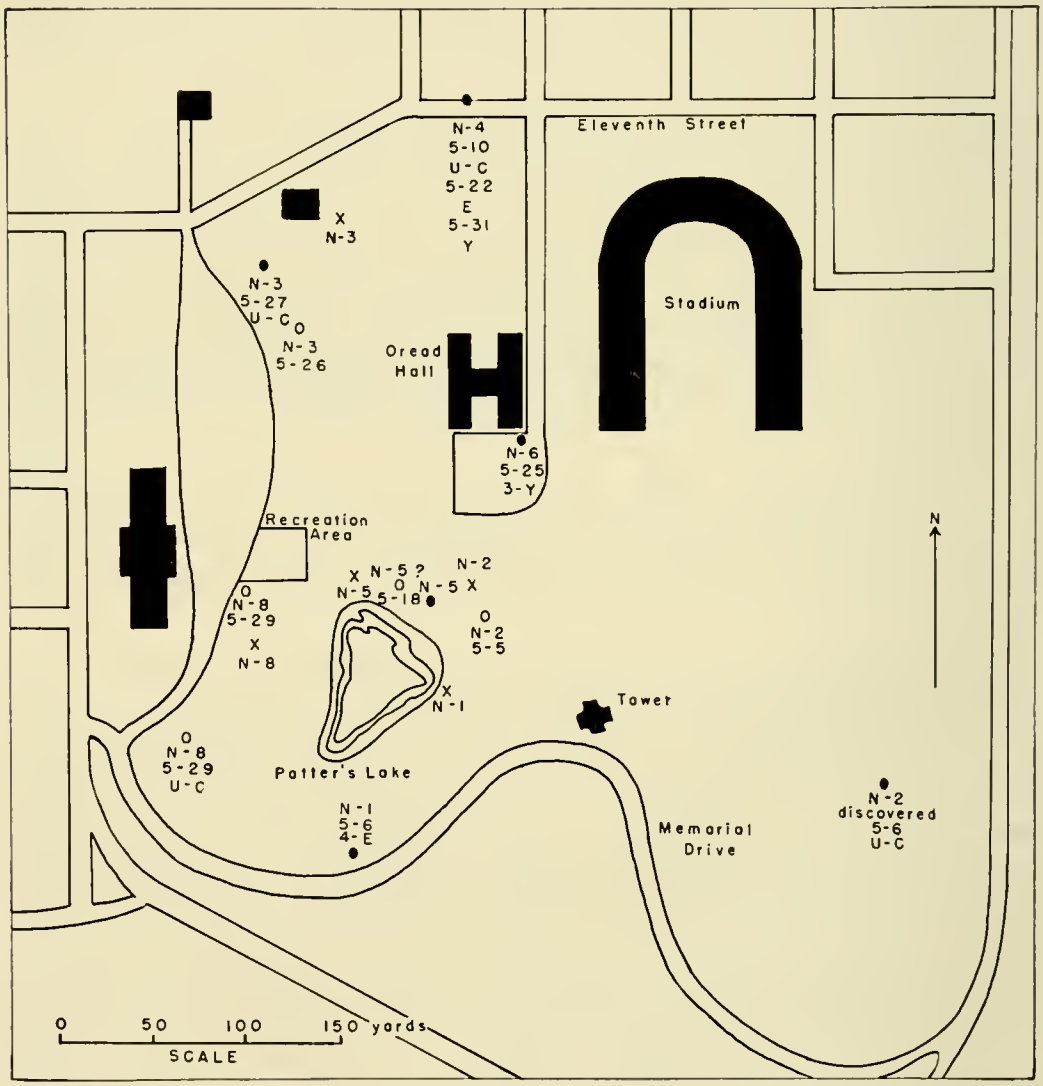


FIG. 10.—Diagram of portion of campus of University of Kansas showing locations of nests, false nests, and other places of activity of Blue Jays in spring and summer, 1957. Key to symbols: ●, true nest; O, false nest; X, nest material gathering place; Numeral—numeral, date (month—day); N, nest (followed by numeral indicating nest of specific pair); E, eggs; Y, young; U-C, nest under construction.

was effected long ago and its maintenance is now apparent only in the failure of flocks to overlap in range.

Territoriality in the Scrub Jay.—The Scrub Jay is a highly territorial species. Territorial boundaries of three pairs that I observed in the Sandia Mountains, New Mexico, met each other broadly (Fig. 13), but on their other sides did not seem to make contact with territories of any other pairs, although other Scrub Jays inhabited the general area under observation. It was therefore difficult to determine the extent of these territories in the directions from the nest in which no defense was necessary. However, when the birds left the vicinity of the nest in these directions, they were quiet and exhibited themselves less, at about where I have drawn "territorial boundaries." Most of the activity of the jays was confined to the areas designated as their territories, except for occasional instances of trespass on their neighbors' areas (which usually resulted in conflict), and regular visits to several areas where territories overlapped. The latter included a well-spring, the only source of water nearby, located approximately at the junction of the three territories, and a grove of oaks several hundred yards up an arroyo from territory N-1 (Fig. 9). The former area seemed to be regarded by each pair as part of its territory. Members of different pairs did not often visit the water supply at the same time. Birds of N-1 and N-2 frequently defended the water hole against each other and against birds of N-3. The latter pair came often to the spring but did not defend it. On the other hand, the oak-grove was not defended, the birds typically being quiet and difficult to locate when there, although their flight to that area was easily traced. The birds frequented the grove in stormy weather, in the heat of early afternoon, and occasionally late in the evening. There is a strong possibility that they roosted there in the early part of the nesting cycle.

The territorial boundaries of these three pairs of Scrub Jays were located according to physiographic features such as that which separated territories N-1 and N-2 (Fig. 12). Territory N-3 was located downhill from the other two territories, and the boundary between N-1, N-2, and N-3 was marked by a shelf of rock just below a stone shelter.

Territory N-1 was 213 yards by 140 yards at its upper end and 100 yards at its lower end, giving an approximate area of 25,560 square yards, or about 5.3 acres. Dimensions of territory N-2 were not measured, but it was approximately the same size as N-1. The

sizes of N-2 and N-3 were not measured because only one side of each was definitely known.

Since Scrub Jays do not sing loudly, proclamation of territory is effected by display and, when called for, by defense. Jays infrequently trespassed on their neighbors' territories; if the owner of a territory was not in the vicinity when a trespasser arrived, there was nevertheless obvious wariness on the part of the interloper. When a flying jay reached the boundary between two territories, it frequently turned suddenly in midair, as if a high wall existed along this "line," even in the absence of residents of the adjacent territory. Large boulders and trees along boundaries seemed to be considered by each pair as part of its territory. Disputes over territorial boundaries usually occurred at these places.

Territorial disputes never included physical contact between contestants but consisted of brief chases, *flitting* displays, and *bobbing* displays accompanied by *br'r'r'r'r'* calls. The *flitting* display consisted of vigorous hopping about with the tail and body being switched from side to side. The head is held erect, the body feathers are closely appressed, and the whole attitude of the bird

FIG. 11.—Typical habitat of the Scrub Jay in the Sandia Mountains, New Mexico.

FIG. 12.—The line of boulders, on a slight rise of ground between two arroyos in the photo, separates two territories of Scrub Jays.

is one of alertness. A similar display is given by male Blue Jays in group courtship of early spring.

In a typical instance of territoriality a bird ventures to the boundary of its territory, whereupon a bird from the adjacent territory appears; the two birds perch in the same tree or on the same boulder along the boundary. The encounter may then involve a threat by each bird toward the other (*flitting, bobbing,* rattling call), but contact never occurs. The encounter is terminated when one bird retreats into its territory; such retreat usually occurs within 10 seconds of the beginning of display. The other bird remains for a minute or more at the boundary giving the *br'r'r'r'r'* call and displaying, though not so actively as when the opponent is present.

Ecological bases of reproductive sociality in Aphelocoma.—In *Aphelocoma,* we may now consider the ecological basis for the

existence of territoriality of pairs of the Scrub Jay throughout much of its range and high degree of sociality of the Mexican Jay in much of its range. Ecological factors possibly have been important in the development of territoriality only in the Scrub Jay of the genus. Although the ecological characteristics of the habitat of the Scrub

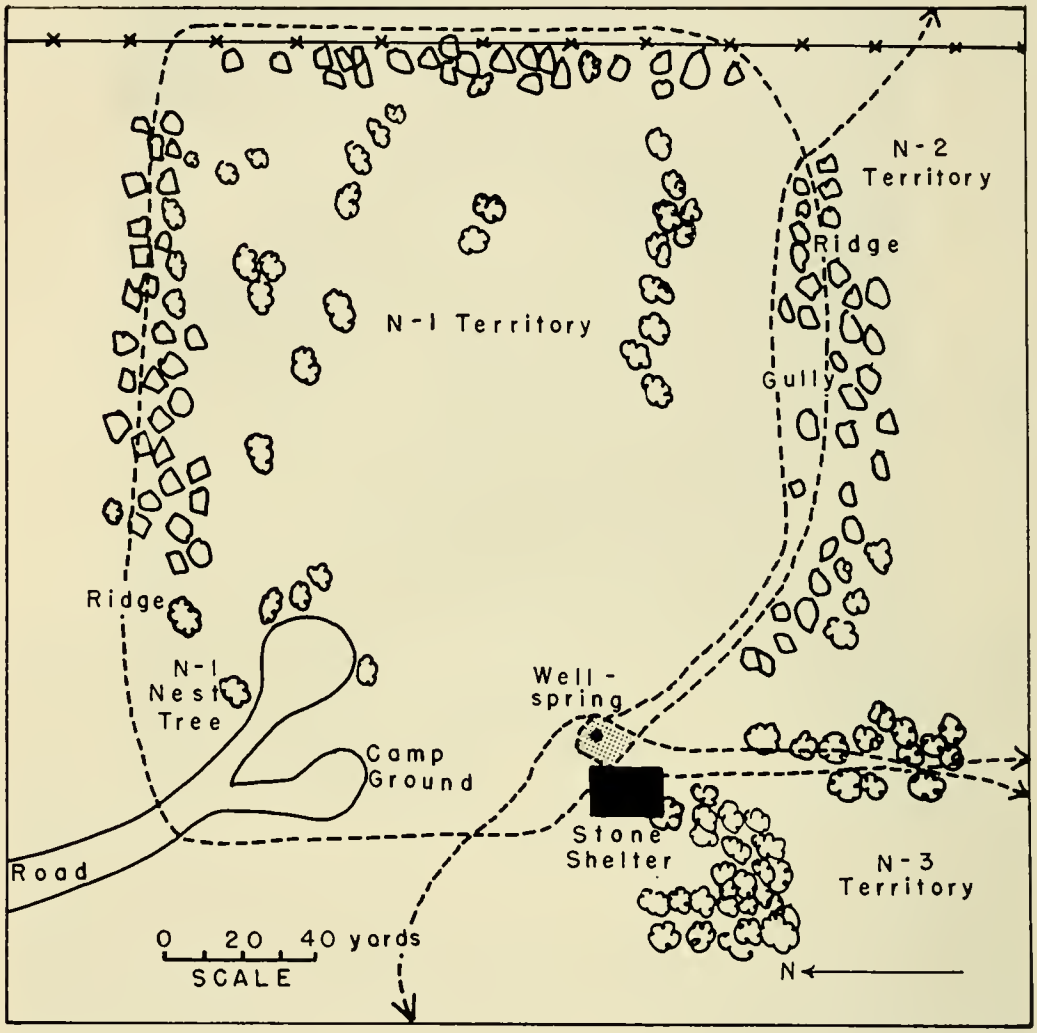


FIG. 13.—Diagram showing interseeting boundaries of territories of three pairs of Scrub Jays in the Sandia Mountains, New Mexico, April 2, 1956. Broken lines represent territorial boundaries. Stippled area is where all three territories overlapped at water source. Only one complete territory, of N-1, is shown.

Jay and the Mexican Jay are varied, it seems evident, as Pitelka (1951:381) has pointed out, that the habitat preference of the Scrub Jay is far less narrow than that of the Mexican Jay. The latter species is confined for the most part to pine-oak vegetation throughout its range. Within this formation, it characteristically shows a preference for the more arborescent parts of the woodland (Pitelka, 1951:384) (Fig. 14), riparian situations being typical.

It is possible that restriction to specific habitats may logically be correlated with highly social breeding habits. In a given region a population of the species may find only a small area suitable to its needs. In order to maintain the population, aterritoriality of pairs may thus be a necessity. The Scrub Jay seems able to exist in "poorer," more xeric habitat, although it does not always do so, invading richer habitat often, when the latter is not occupied by the Mexican Jay. The tolerance of the Scrub Jay for poor habitat is exhibited well in southeastern Arizona. In the Chiricahua Mountains, the species is rare except locally (for example, in the foothills near the town of Paradise). The jay occurs in isolated single pairs high on relatively bare sides of the canyons, and in dry foothills with pinyon pine (*Pinus edulis*). In these mountains, the Mexican Jay occupies the vegetationally richer canyon floor. Whether the two species occur sympatrically or not, the Mexican Jay seems obligated to the richest, most arborescent portion of its range; the bird's ecological requirements are thus probably more strict than those of the Scrub Jay.

If we combine the last assumption with another—that the species has a minimum population size below which it could not survive, we arrive at a possible reason for the lack of territoriality in the Mexican Jay. Ordinarily, territoriality is thought of as functioning in the survival of a species. If, however, the Mexican Jay were territorial, with the some spatial requirements per pair as the Scrub Jay but with its present ecological requirements, the combination of these two sets of limiting factors might prevent the species from maintaining the population above the minimum level necessary for survival. This argument supposes a minimum population size, N, that in territorial species represents the breeding population. But N in a species such as the Mexican Jay must represent the breeding pairs plus the non-breeding birds that live with the breeders, contributing toward reproductive success by helping to build the nest and feed the young, and probably affording increased protection from predators and ensuring success in other ways. We must assume this contribution, since if we do not the prevalence of these assisting birds is difficult to explain as having selective value to the species.

The Scrub Jay, on the other hand, exhibits the alternative in its habits—territoriality of pairs with invasion of a wide range of habitats, except for the subspecies in Florida. The habits of the Scrub Jay in Florida are perhaps unique in the species in seeming

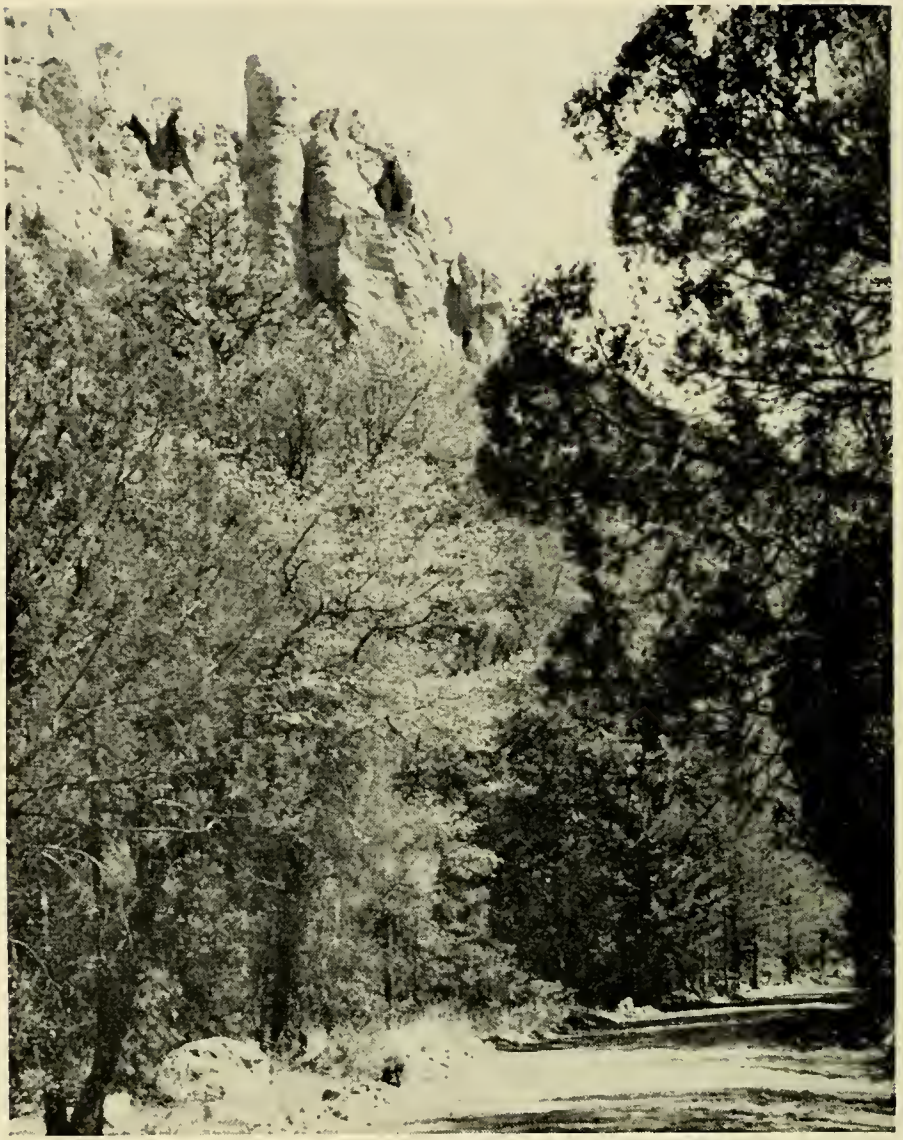


FIG. 14.—Typical habitat of the Mexican Jay in South Fork Canyon, Chiricahua Mountains, Arizona. Note richness of vegetation compared to Scrub Jay habitat, Figure 11.

narrowness of habitat preference; this narrowness correlates well with the possible relationship between strictness or narrowness of habitat preference and the existence of highly developed sociality. *A. c. coerulescens* is restricted to scrub vegetation and does not occur in pine woods, hummocks, or swamps (Pitelka, 1951:316), as do populations of other races of the species. These other habitats are present in the range of the jay in Florida and are seemingly available for occupying by the jays. Because of restriction to scrub vegetation, we might expect the Scrub Jay of Florida to possess a higher degree of sociality than territoriality of pairs, as, indeed, it does.

Copulation and Related Activities

Copulation in the Blue Jay occurs in the final stage of nestbuilding. It is preceded by a gradual cessation of nestbuilding activities and the appearance of precopulatory posturing and display.

Precopulatory behavior in the Blue Jay.—A day or so before copulation takes place, the female Blue Jay becomes broody; having brought a piece of material to the nest, she sits on the structure for several minutes at a time. She also solicits food more often and with greater intensity than she did previously. She frequently begs while on or near the nest and almost always begs when the male appears near her or the nest. Courtship feeding serves to stimulate the tendency to behave sexually in both male and female; this behavior in turn strengthens the pair-bond. (After copulation, courtship feeding also helps maintain sexual interest and consequently helps maintain the pair-bond through the breeding season.) The tendency to behave epigamically is at its height at the time of copulation; not only is courtship feeding most frequent then, but at the peak of sexual excitement the begging behavior of the female is intense to the degree that it may be termed copulation soliciting behavior. Soliciting behavior elicits from the male a response different from that elicited by begging, demonstrating the distinctness of these two similar types of behavior in the female.

The drive of the male in courtship feeding behavior seems to be consummated by contact of his bill and that of the female; transfer of food does not seem necessary. The copulatory tendency of the male seems to be satisfied, however, in action involving fuller contact of the birds, accomplished through mounting.

It has been stated that food-begging behavior and copulation soliciting behavior are similar, and that the latter is probably derived from the former. There may be intermediate responses by the male to begging of intermediate intensity by the female. I once observed a pair of Blue Jays, in the late nestbuilding phase, engaged in a peculiar display that I have termed the *nudging* display (Fig. 16). *Nudging* may be the means by which the male consummates a contact drive of intensity intermediate between copulatory and courtship feeding contact drives. Although copulation did not take place after *nudging*, fluffing and preening of the feathers and vigorous feeding—all associated with postcopulatory behavior—were seen. In addition, the nest was nearly completed, the female was broody, and the time for copulation was near for this pair.

In the *nudging* display, the two birds sat side by side on a limb,

the female fluffed and seemingly broody, the male with throat distended and body hunched forward. The male then edged over to the female and gently pushed against her side; she retained her posture. He gradually moved her a short distance along the branch by his pushing action. Neither bird gave any vocalization. After this display, which occupied only a few seconds, both birds flew into a nearby tree and foraged more actively than in normal feeding behavior. The female occasionally interrupted foraging with vigorous preening.

Copulatory and associated behavior in the Blue Jay.—Blue Jays copulate in trees. Just before copulation, the female assumes the copulatory pose (Fig. 6). This posture, as mentioned, is an intense form of the begging posture (Fig. 5) associated with courtship feeding, but here the tail is held angled upward and slightly spread, the wings are extended forward, and fanned at the wrist, and the slightly-opened bill is directed upward toward the male. The posture of the male is stiffly erect, with crest raised, wings closely appressed to the body, and the bill pointed downward toward the female (Fig. 15). Typically, the female retains the copulatory posture and gives soliciting calls—*kueu kueu,* and as the male mounts, her calls become more intense. Copulation lasts for about four seconds, after which the male departs and the female remains perched for a few seconds, preening her wings. She then may go to the nest and sit briefly, as she does regularly in this period of the breeding cycle. Both birds engage in fluffing and preening the feathers and in vigorous foraging as part of postcopulatory activity, as mentioned previously.

The act usually occurs near the nest on a large horizontal limb, but on one occasion, I observed copulation between two birds that were strangers in a particular study area, in the territory of another pair. In this instance the resident male three times prevented copulation by swooping down upon the strange birds. Copulation was finally achieved and the fourth attack of the resident male caused the copulating male to fly away. The attacks then ceased, and the strange female was allowed to remain perched and preen and fluff for nearly five minutes.

It will be recalled that Blue Jays are territorial toward other jays that feed, or are otherwise active, in another jay's territory as if they "belonged" there. Doubtless, copulatory activity by two birds indicates that they "belong" in the area where they are copulating; hence the aggressive reaction of the resident male.

Behavior in the Blue Jay During Egg-laying and Incubation

Transition from nestbuilding.—The transition from nestbuilding to egg-laying and incubation is a gradual one. "Nest-sitting" is perhaps the earliest element in the transition; such sitting by the female Blue Jay begins in the false nestbuilding stage, when only a mere platform of sticks exists. While the nest itself is being constructed, the female frequently crouches on it, and as the nest nears completion she spends more and more time in this activity. The male, who has been feeding her all along, increases the frequency of feedings as the nest nears completion. Courtship feeding becomes obviously functional now, allowing the female to remain on or near the nest for greater periods of time. This will help assure more nearly continuous incubation and will reduce the possibility of loss of eggs to predators.

Participation of the sexes.—Only the female Blue Jay sits on the nest in this phase of the breeding cycle. This is typical of most, if not all, corvids (Amadon, 1944a:2). In this period the male feeds the female at or near the nest, forages casually in the area, acting as a guard for his mate and the territory against other jays and predators, and stimulates the female to remain on or near the nest by his frequent visits to the nest with food.

Incubation is interrupted frequently by the male feeding the female or by the latter leaving the nest to feed, preen, or merely perch in the vicinity of the nest. In most cases, the female leaves the nest to be fed by her mate only early in incubation; she tends to remain on or near the nest to be fed in the later stages. At all times, feeding takes place within a few feet of the nest or in a nearby tree. Afterward, the male nearly always remains near his mate until she returns to the nest. If she chooses to stay off, the male accompanies her.

At one nest, the female sat for 55 out of 60 minutes (5:00-6:00 p. m.), leaving the nest only once and being fed twice by her mate while off the nest. The next day in 60 minutes (6:55-7:55 a. m.) she sat for 46 minutes in periods of 8, 25, 12, and 1, leaving the nest for periods of 3, 5, and 6 minutes. The first two times off she was fed by the male. The last time off she joined her mate in chasing a squirrel.

These are typical examples of activities early in incubation. From the middle of the second week until hatching, the female sits for longer periods, whether or not she is fed by her mate. At one nest

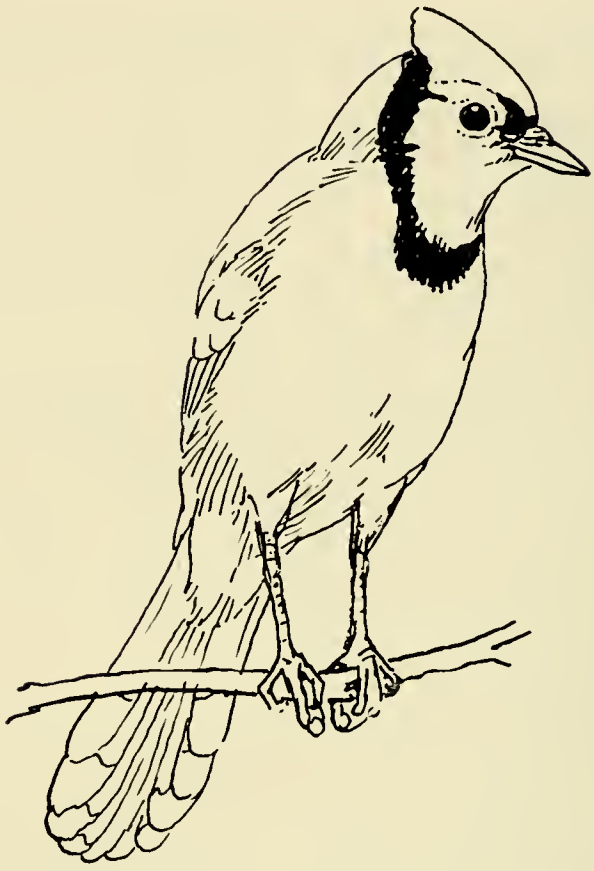


FIG. 15.—Precopulatory posture of the male Blue Jay.

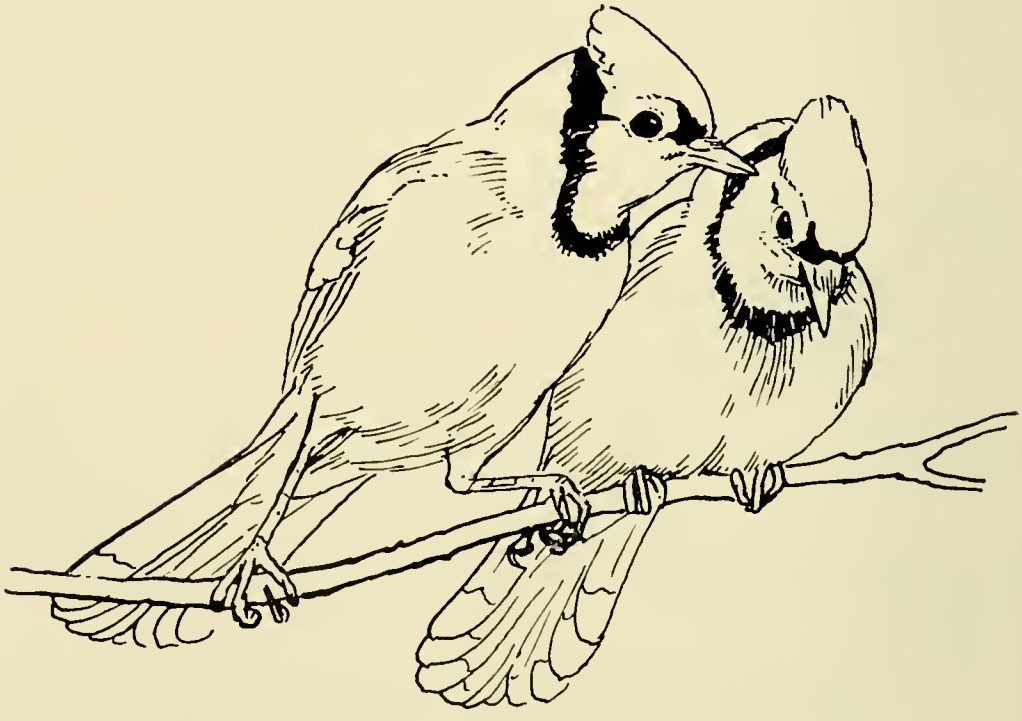


FIG. 16.—*Nudging* display, possibly precopulatory behavior. Female on left, male on right.

in midincubation, the female sat for 59 of 60 minutes, coming off only to preen and stretch near the nest; she was fed twice by her mate. The following day she was observed to sit on the nest for 113 out of 120 minutes, leaving the nest once to stretch and preen. She was fed by her mate once, at the nest.

In late stages of incubation the only change is toward longer periods of incubation and a greater reluctance of the female to leave the nest for any reason. For example, in early incubation at one nest, a stuffed Long-eared Owl (*Asio otus*) placed prominently in the nest tree elicited a general alarm bringing the female from the nest, her mate from his activities, and other jays from the surrounding area to mob the owl. In middle and late stages of incubation, the same owl seldom caused the female to leave the nest, although mobbing action still occurred on the part of other jays. At one nest in a late stage of incubation, in an observation period of 130 minutes, the female was off the nest 2.3 percent of the time (once for 3 minutes) and incubated 97.7 percent of the time (two periods of 90 and 37 minutes, respectively). The following day in 160 minutes of observation, the female was off the nest 3.1 percent of the time (once for approximately 5 minutes) and incubated 96.9 percent of the time (two periods of 20 and 135 minutes, respectively). In her times off the nest, she preened, fluffed, stretched, and foraged. This female lost her mate sometime in early incubation and so was never fed at the nest. She foraged for herself, and late in incubation acquired a new mate. Although this latter bird was not collected, it seemed to be a first-year male. The significance of the acquisition of new mates is discussed previously under Comparison of Courtship Habits and Pair-bonds.

The female Blue Jay's periods away from the nest in the phase of incubation are not primarily for purposes of foraging, but are for the most part spent in flying about, stretching, preening, and otherwise rearranging the plumage. Only when the male is not attentive does the female do a greal deal of foraging for herself. Since she is relatively inactive, she probably requires much less food than otherwise, and seems, in fact, to get little food. I noted on several occasions that contact between the female and male of a pair at the nest did not involve feeding at all.

It seems that in almost any instance of such feedings there are two functions, one ritualistic or symbolic and involved with creation or maintenance of the pair-bond, the other nutritional in making food available to the female. Emphasis is on the first function

until nesting begins and on the second one afterwards, but at no time is the act devoid of both. The fact that the ritual may be performed in the period of incubation without actual transfer of food, serves to emphasize the continued presence of the ritualistic basis after pair-formation. Presumably the need for maintaining the pair-bond is still important and perhaps can be effectively accomplished only through the stimulus provided by the presence of mutual interests of the pair—the nest, eggs, and young birds. Particularly does this seem logical in a species where the female performs all the duties of incubation and in which there are no other ritualistic displays that may be connected with maintenance of the pair-bond; it is possible, then, that the male remains an integral component of the breeding cycle at this time only by the continued stimulation he receives from contact with the female.

Behavior in the Mexican Jay During Egg-laying and Incubation

Two birds were involved in incubatory duties at a nest of the Mexican Jay observed by Gross (1949:246). The flock associated with this pair in nestbuilding maintained interest in the nest in early incubation, occasionally coming there and investigating the eggs. These visitors were often so intent on investigating the nest that they dislodged the female by nudging her and by grasping her beak if she resisted their attempts. Later in incubation, only the presence of the observer at the nest exciting the incubating bird caused the flock to assemble at the nest-site.

My own observations of egg-laying and incubatory behavior of this species are limited to those made at one nest in June, 1956. This nest was discovered soon after the clutch of four eggs had been completed. This was an unusually late nesting (June 4), the dry season having set in several weeks before. The remainder of the population of jays in the vicinity of the Research Station had completed breeding or were feeding young out of the nest. As a result, the nesting habits of this pair may not have been typical of nesting habits at the height of the breeding season, as the observations above indicate.

Participation of the sexes.—From June 4 until June 18, when three of the young hatched, only one bird, presumably the female, was ever seen at the nest. She was never fed by another jay near the nest, and when she left the vicinity of the nest she was not attended by another jay so far as I could determine. Other jays

were observed to come near the nest three times in the period of incubation. Two of these times were on occasions when I had placed a mounted bird on a limb near the nest. When a mount of a Long-eared Owl was placed there, the female and three other jays (two with parti-colored bills) flew into trees near the nest-site. They did not enter into mobbing of the owl, but merely remained as interested bystanders while the female scolded and dived at the "enemy." When a mount of a Blue Jay was placed near the nest, a single other Mexican Jay investigated it. The third occasion when other birds besides the female appeared at the nest occurred when I once disturbed the female, causing her to call in alarm. Then, another excited jay flew into the nest tree, called *reek reek*, and investigated me.

Attentiveness.—The nest was located at the edge of a road used by as many as six cars a day. The incubating female never grew accustomed to the cars; as often as not she bounded from the nest as they passed. My presence on foot in the vicinity also excited her. Any slight movement on my part while she was on the nest caused her to leave. But for these interruptions, her incubation periods would doubtless have been longer. In a 120-minute period of no disturbance on June 14 (1:30 to 3:30 p. m.) she was off the nest 16.7 percent of the time (2 times of 8 and 12 minutes, respectively) and incubated 83.3 percent of the time (2 periods of 70 and 30 minutes, respectively). At 7:30 p. m. the same day, the female was on the nest. On June 13, in a period of 132 minutes (1:33 to 3:45 p. m.), she was off the nest 11.4 percent of the time (3 periods of 11, 2, and 12 minutes, respectively) and incubated 88.6 percent of the time (4 periods of 31, 15, 26, and 35 minutes, respectively). The two middle periods of incubation probably would have comprised one period if I had not accidentally frightened the female from the nest.

In early morning hours, the female was more reluctant to leave the nest, and her periods of time away from the nest were shorter than in the afternoon.

Behavior at the nest.—Unlike the Blue Jay, the female Mexican Jay exhibited no stealthiness at the nest. Almost always when arriving at the nest or leaving it, and occasionally while sitting on it, she gave the *reek reek* call. It was obvious that some of these times she had not been disturbed by anything; these calls may have been assembly calls given to a mate or members of the feeding flock that inhabited the area. Often her calls were answered from some

distance up or down the canyon, and these answering calls seemed to attract the female. Thus the vocal exchange may have functioned in orientation of the female toward other members of the flock. When she left the nest, she did not remain in or near the nest tree, as is often characteristic of female Blue Jays at the time of incubation, but flew out of that vicinity to feed and rest.

No marked changes were observed in the attentiveness of the female from early to late incubation, in contrast to the habits of the Blue Jay.

Discussion and Summary of Incubatory Habits

In the Blue Jay and in the Scrub Jay, according to Amadon (1944b:12), the female is fed at the nest by the male. Such feeding does not always occur in the Mexican Jay, nor is a male always attentive, or even in evidence near the nest, throughout incubation. Amadon (1944b:12) did not observe feeding of the female Scrub Jay by the male away from the nest but believes that it probably occurs. Such feeding does occur in the Blue Jay, particularly in the early stages of incubation. Feeding of the female by the male at any time in the Mexican Jay probably is not common as in the Blue and Scrub Jay.

Compared to the Mexican Jay, the Scrub Jay and Blue Jay are highly secretive in the vicinity of the nest. The former frequently calls in a loud voice at the nest, while the other two are silent or utter only low conversational notes at the nest. In behavior at the nest, the Scrub Jay and Blue Jay resemble each other more than either resembles the Mexican Jay.

Care of Young by the Blue Jay

Early nestling stage.—The duration of periods spent by the female Blue Jay on the nest in late stages of incubation increases greatly as the time of hatching nears. Much of the food that the female receives at this time is brought by the male, who proceeds to feed his mate at or near the nest. For the male, feeding the female at the nest is closely linked with feeding of young birds immediately after hatching; the behavior of the male in these two functions differs hardly at all. The principal change in behavior occurs in the female. She continues to beg from the male and receives food precisely as before hatching, but the movements of the young beneath her and their gaping mouths when she arises from the nest are stimuli causing her also to bring food to the nest. Both adults, then, respond to a begging, gaping stimulus, now

provided primarily by the young birds. It will be recalled from the discussion of courtship feeding that the male did not gape in response to the arrival nearby of his mate, and this failure was seemingly the factor preventing the female, in turn, from attempting to feed her mate. The gaping young provide this stimulus to the female. She still broods a great deal, remaining on the nest almost as much as before hatching, since the nestlings, once fed, do not gape, and offer stimulus (warmth, inactivity) for brooding.

The female feeds, preens, and occasionally perches for several minutes in a tree near the nest, while not feeding or brooding the young. The male always remains in the vicinity of the nest, visits it occasionally, and chases away other jays and squirrels. These activities remain fairly constant until after about the first week.

The male never broods the young in early stages of their life and rarely ever does so. Each feeding of the nestlings by the female is usually followed by a period of brooding at this stage.

The practice of nest-sanitation is begun by the second day. The fecal matter is sometimes eaten at the nest, but later it is carried away; it then may still be eaten, since I did not observe fecal sacs to be dropped by the birds.

By the fourth day after hatching, the contribution of the male to feeding of the young increases somewhat. A male at a nest with young four days old was observed to feed the nestlings five times and the female two times in 60 minutes. The female in this time brooded for approximately 29 minutes. The male brooded, too, for eight minutes while the female was away from the nest to get food for the young the first time.

The male continues to feed his mate at the nest. Sometimes he fails to deliver to her the food brought, and she is thus stimulated to rise from the nest if she has not already done so. After she arises, the male may then feed the young. The male presents food without much stimulus from his mate, as the female's begging is weak at the nest. While feeding the young, the adults are quiet except for low conversational notes, *kut kut*, and an occasional begging call given by the female.

There are never more than two adults caring for a brood, in contrast to the case in the Mexican Jay. Territoriality continues to be expressed toward interloping jays behaving in the same way as the resident pair (probably in the same phase of the breeding cycle).

Behavior after the first week of care of the young.—By the end of the first week, brooding is restricted mainly to nighttime, midday, and midafternoon, except in unseasonably cool weather when brooding may occur at any time and for periods up to two hours in length.

The contribution of the male to feeding of the young is generally greater than before this time, and there are occasional days when he assumes a major share of this duty. On the fourteenth day after hatching at one nest, in a period of 180 minutes (6:45-9:45 a. m.), the male brought food to the young 18 times, the female twice. Moreover, the female begged the male for food almost every time he visited the nest; she closely followed him about, or sat on the rim of the nest most of the day. She also contributed to care for the young by occasionally removing feces and by giving a part of the food received from the male to the young. Once she took food from a nestling and ate the morsel. Three days later, division of duties was nearly equal at this nest; the male fed the young five times and the female four times, in 140 minutes.

The sexes probably participate about equally in feeding the young, but the previously mentioned tendency for irregular contribution to care for the young by either sex from day to day seems characteristic of the species. In all cases observed where one or the other adult failed to feed the young or fed them only a few times in a period of observation, the nonfeeding bird contributed to care of the young by performing other tasks, such as removal of feces, guarding of the nest, and brooding.

I did not discover the reason for these failures to feed the young by either sex on a given day. Particularly puzzling was the peculiar behavior of the female that almost ceased to feed the nestlings and simultaneously reverted to begging her mate frequently in a manner characteristic of courtship. She was unquestionably a member of the pair owning the nest; no other adult birds appeared at the nest at any time. Her begging behavior was abnormal, of course, only in the fact that it occurred too frequently for this period of the breeding cycle. Such abnormal behavior was otherwise not observed in Blue Jays in this study. Resisting the temptation to classify this behavior as neurotic, it is perhaps best to call it displacement begging (such reversions to behavior of a previous phase of the cycle are frequently characteristic of displacement behavior). The causative phenomenon might have been conflict between drives to feed the young and to be fed by her mate. Perhaps the

crucial moment in this conflict occurred only briefly earlier in the day when the drive to be fed by her mate failed to be consummated. This failure then could have upset the normal course of behavior for this phase of the life cycle on this one day. It seems probable to me that other irregularities in participation in care of the young by the sexes may be attributable to similar subtle disturbances of the delicate balance of interaction between the adults.

In early stages of care of the young, most feeding activity occurs in the morning hours. But after a week, feeding sometimes continues even in the hottest parts of the day. On the afternoon of the day on which the male performed most of the feeding, the male fed the young five times and the female brooded once for two minutes in a 60 minute period of observation. Generally, feedings in the afternoon hours average little more than one per hour.

Late nestling stage.—Frequency of feeding of the young continues at about the same rate in the last week of care of young, until the latter leave the nest (between the 17th and 19th days after hatching). Brooding is confined to night and brief periods at irregular intervals in the day. At one nest, the male fed the young five times, the female four, in 140 minutes of observation on the day that the young began to leave the nest. However, at another nest with young estimated at 16 days of age, the male fed the nestlings four times, the female twice, in 120 minutes. The latter nest was near a walkway and road, and the infrequency of feedings in the two hours may have been a result of the adults being frequently frightened by passersby.

Throughout the nesting season, but particularly in the last days before the young are fledged, the adults show little timidity when near the nest. Comparative lack of vocalization by the adults in the vicinity of the nest affords protection of the young and nest. The parent birds also readily attack any predator that ventures near the nest.

Beyond the age of about 15 days, the young birds become restless and move about in the nest, stand up in it, and even perch on its rim. The female occasionaly attempts to brood them and achieves a sort of halfbrooding position (Fig. 17). This position is seldom maintained for more than five minutes at a time, for the young squirm about, peck at sticks in the nest, and invariably jostle the female loose when her mate arrives with food. By the 17th and 18th day after hatching, the young move to the rim of the nest even when resting, and then begin to venture out onto nearby branches.

The birds have engaged in wing flapping from the second week of life, but only when the adults brought food. Now they sit near or on the rim of the nest and exercise their wings vigorously when the adults are not about. This exercise soon leads to the first attempts at flight by the young.

Fledgling stage.—Adult Blue Jays are cognizant of territorial boundaries until the young leave the nest, as I have previously discussed. But once the young have flown, their aimless rovings govern the movements of the adults, and the family group may range over an area several times the size of the territory. The first flights of the young are taken by chance at different times and in different directions; brood-mates are thus separated for a short time. After the young attain flying and navigational ability the brood is reformed and seems to remain more or less a unit for the remainder of the summer. Loose family groups are prevalent in August and September before the flocks of autumn are formed.

The adults continue to feed the young for several weeks (as long as one or two months, according to Laskey, 1958:213) after they leave the nest, or into the period of postjuvenal molt, when independent feeding habits begin to develop. The fact that the young usually remain close together improves their chances of being fed regularly; young out of the nest for at least two weeks frequently are seen perched side by side. Broods certainly away from the nest for over a month are frequently seen calling to their parents from the same tree and flying in a loose group from one grove to another following an adult that is searching for food. Adults seemingly continue to feed the young at the same frequency as before the nest was vacated. The lack of any further recognition of territoriality is important in the wanderings of the family group, because its members may trespass without conflict in the territory of other jays that have eggs or young still in the nest.

Care of the Young by the Mexican Jay

In care of young Mexican Jays observed by Gross (1949:247) at one nest, only two adults were involved. The young were brooded in the first week and were left alone only infrequently when both adults were searching for food simultaneously. The male and female shared equally in care of the young, which left the nest at approximately 25 days of age. Gross observed other nests located in the vicinity of the one discussed above, two such nests not more than 75 feet away. At these nests each pair seemed independent

of the others. Nest sanitation was practiced, the adults swallowing fecal saces when the young were first hatched, and carrying these sacs away after the young were older.

Most of my observations of care of young by Mexican Jays were made after the young left the nest. The few observations made in early as well as late stages indicate some striking differences in the behavior of Blue and Mexican Jays, and certain differences in the care of the young as observed by Gross and by me.

Early nestling stage.—At the nest where my observations were made through most of the period of incubation, the female, as mentioned, received no help from any other adult, nor did other adults ever appear at the nest. However, on the day of hatching two additional adults appeared in the vicinity of the nest, and one of them made visits to the nest to feed the female there. The latter bird was excited, brooded the three young (and one remaining egg) for short periods, and flew about calling excitedly at other times. She displayed the same lack of caution about the nest as in the period of incubation. On several occasions, she flew to the rim of the nest, and then began a display of rapid fluttering of the wings accompanied by begging calls given with the bill open. At these times, another adult followed her, landing a short distance from the nest. The other bird, presumably a male, hopped to the rim of the nest when the female began to beg and seemingly fed the young as the female stood by. Afterwards, the female brooded

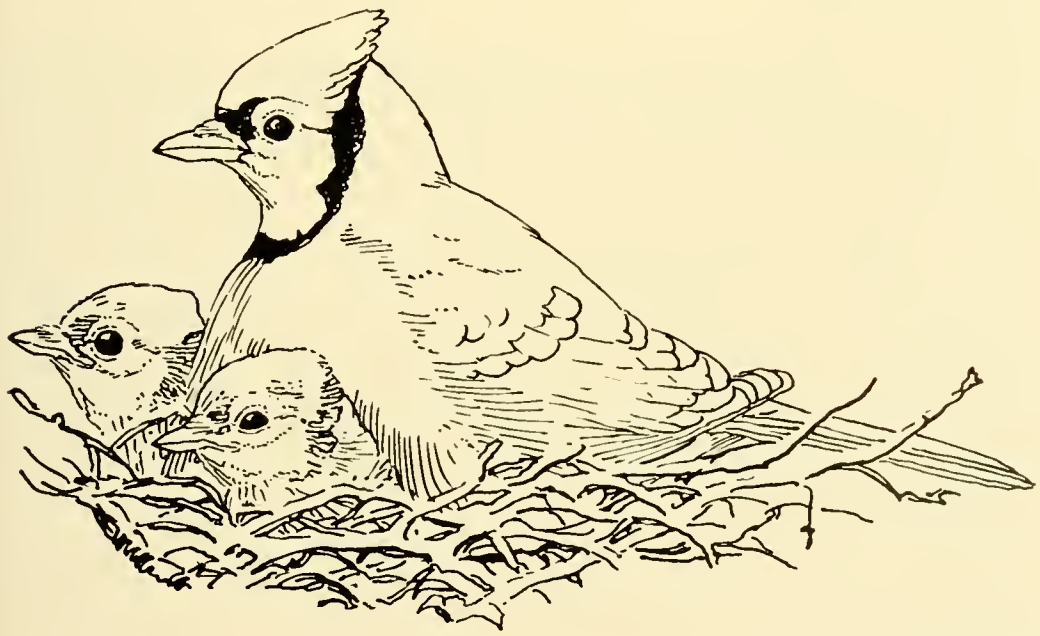


FIG. 17.—The half-brooding position of a female Blue Jay in late stage of caring for nestlings.

while the male sat in the top of the nest tree for ten minutes. If another adult came near the nest while the female was away, she always hurriedly returned, and gave the begging display until the other bird came to the nest or flew away. On one occasion, both adults left the nest in one direction, after which another adult appeared in the nest tree from a different direction. The female returned hurriedly, calling loudly, and both advanced to the rim of the nest, simultaneously. The strange adult seemed to feed the young while the female watched. The latter brooded after this episode. The begging call of the female is a soft *kwaaa kwaaa kwaaa.* I twice saw a bird feed the female at this nest; on one occasion, she quickly stood up and gave the food to the young, and the other time she ate the food herself.

At the above nest, the young died on the second day after hatching. The nest was a late one; the young hatched after the dry season was well advanced. The breeding activities of the Mexican Jays in the area as mentioned previously consisted only of adults feeding young already out of the nest. The adult birds at the present nest gave several indications that they were unable to find proper food for the young, which seems probable, since only small soft-bodied insects would be suitable, and these were certainly at a premium.

Two characteristics described above are not found in the Blue Jay. These are: More than two adults attentive at a single nest, and lack of caution of the adults when near the nest. Both characteristics persist in Mexican Jays through the remainder of the nesting activities.

Middle nestling stage.—I made few observations on care of the young in the first or second weeks of their lives. I discovered two nests, one with eggs and one with young, in the Chiricahua Mountains, when most of the adults in the vicinity were still building nests. These two nests were within 100 feet of each other. The flock of perhaps eight birds that inhabited the grove containing these nests was composed entirely of adult (black-billed) birds. In a period of observation of 60 minutes at the nest with young birds, feeding occurred three times, the young each time giving the call characteristic of young captive Mexican Jays. This call is harsh and squealing.

Fledgling stage.—After the young leave the nest, the adults continue to feed them for at least five weeks, a protracted period of postnestling care similar to that in the Blue Jay. As with the lat-

ter species, independent feeding behavior appears after this time, along with the inception of postjuvenal molt.

The number of jays at least a year old that accompanies a group of three or four juveniles soon after they leave the nest is remarkable. The attending birds include some individuals with wholly black bills, others with parti-colored bills; these are, generally, adults and subadults, respectively. One such group contained four juveniles and approximately ten other birds, five of which were never seen to feed the young but nevertheless remained close by, shrieking at and mobbing persons that came close to the young. All of these birds, then, formed a company whose activities centered around the welfare of four young birds. I have recorded as many as four different birds feeding the same young within ten minutes.

As in the early stages of care, the birds caring for the young are not cautious, making the flock easy to find. But the flock is not easily watched, because the birds move about considerably, and the young, although they occasionally sit close together, may disperse throughout a grove of trees. The young are seldom silent, giving a begging call like that of young Starlings *(Sturnus vulgaris)* when soliciting food. Both adult and young Mexican Jays give *reek reek* calls of alarm and assembly, and soft *kwot kwot* conversational calls that are seemingly low intensity forms of the *reek* call.

The attentiveness of the adults toward the young fluctuates greatly. In early morning hours feeding is at its peak, but there is a period of an hour or so before noon when activity is low. At this time all the birds can be found sitting quietly in trees. There is a period of increased activity for two to three hours in the afternoon, but activity after this declines, and the birds seem to disperse after about 3:00 p. m. No further feeding of the young occurs.

I have mentioned previously that a late-nesting pair seemed to have difficulty obtaining small soft-bodied insects for their newly-hatched young in the dry season. Adults with young out of the nest at the time the dry season becomes severe are not faced with this problem, for although insects remain scarce until the rains begin in late July, small lizards are plentiful, and these seem to form a large part of the food given to the young. The adults catch the lizards and then tear at least the larger ones into pieces before giving them to the young.

PART II.—NONBREEDING BEHAVIOR

BEHAVIOR OF CAPTIVE JUVENAL JAYS

Behavior of Young Blue Jays in Captivity

The study of young jays in captivity afforded the opportunity to observe the development and maturation of many behavior patterns evident in wild adults of the species. The difficulties experienced in the study of captive adults were nearly absent in studies of young, since the latter were much tamer and in consequence behaved much like their counterparts in the wild. In this study, two young Blue Jays were hand-reared from the late nestling stage, one through the postjuvenal molt (or, from about 19 to 62 days of age) and the other to the age of approximately 118 days. The birds were nestmates.

No attempt was made to transform either of the young Blue Jays into "household pets." Rather, an attempt was made to maintain a type of treatment that would cause the birds to remain tame but not friendly to the degree that they "regarded" themselves as humans.

Throughout their lives in captivity the birds were fed raw horse meat and a mixture of commercial dog food and vitamin supplement. From time to time they were given other foods such as peanuts, grasshoppers, and other insects. The latter three foods were offered especially in that period when the motor patterns of self-feeding and play were becoming evident.

The birds were retained in a small cage in my laboratory, but they were given daily freedom of the room for up to two hours at a time. At the approximate age of 54 days, they were transferred to an outdoor cage measuring 8 by 5 by 5 feet. One of the birds was later placed in a 9 by 12 by 6 feet outdoor cage.

Flight.—The broodmates of the captives left the nest within two days of the time I captured the latter birds. As Rand (1937:30) has suggested, young Blue Jays leave the nest before they can fly. The fledglings begin frequent exercising of their wings in captivity at about 27 days of age, the periods usually occurring in the evening just before dark. Less often, vigorous exercising of the wings occurs in the morning hours an hour or so after the first feeding. These periods may be correlated with renewed energy supplies afforded by the food. Immediately after being fed, the young usually are drowsy for a period of 15 minutes to an hour before becoming active. Before the frequent wing exercises are indulged in regularly, the birds are unable to fly at all well. Upon their

release from the cage they flutter weakly along a table top or to the floor to cower in a corner. If placed on a perch, they usually are content to remain there with no attempt to fly.

In the periods of exercising the wings, the jays become considerably wilder than at other times. If the cage door is opened, they attempt to escape, refuse food, avoid being touched, and even threaten an observer. Ability to fly in a partially sustained manner first occurs when the jays are approximately 30 days of age, although each time they are released from captivity previous to this time, they exhibit progressively greater strength so that eventually they do not always flutter downward. At about 30 days, however, young jays exhibit the tendency to escape; if the door to their cage is left open momentarily they attempt to fly out and upward to a perch away from the observer. In these early successful flights, although the forward upward progress of the birds is strong, navigational ability is poor. They usually arrive at a general destination rather than at a specific predetermined point. Rand (1937:30) noted similar cases where the jays, although they flew strongly, perched on precarious and unsatisfactory perches for a time until greater navigational powers had been attained. In these early flights, the birds frequently fly headlong into window panes and even into walls. If they fall to the floor they are unable to take off again but hop rapidly to a place where they can climb higher and launch themselves.

The lag of co-ordination behind strength of flight lasts as little as two days; at 31 days, the jays are difficult to catch once they have escaped the cage. Immediately after escape, they usually fly wildly, presumably until their energy has been somewhat dissipated, and then become quiet and select a perch. If not disturbed, they remain perched for several hours without again flying. Seemingly the confinement of the birds increases their urge to fly, but once "freedom" has been secured, their drive to escape regresses rapidly. Rand (1937:30) noted that his captive young jays always flew to the higher perch-sites in a room. He assumed it to be a behavioral adaptation to keep the birds away from ground predators.

Extension and vigorous flapping of the wings strengthens and co-ordinates the musculature. Wing-flapping is a basic intention movement of flight in these young birds, just as *bobbing* may be an intention movement of flight in adult jays. The young jays never bobbed.

Feeding.—When first removed from the nest, young Blue Jays will not accept food from the hand. But after several hours in

which morsels are frequently poked at their bills and simultaneous squeaking sounds are made with the lips, the birds finally respond strongly, although irregularly at first, by gaping, quivering their wings, and accepting food from the forceps. Often the birds must be offered food repeatedly over a period of several minutes before they will respond. The irregularity of response is not due to degree of hunger. The difference between a "correct" and an "incorrect" presentation of food is slight indeed. Acceptance of food takes place from almost any angle, with or without accompanying squeaks, at sudden and slow presentations, and often after repeated offerings in what seemed to be exactly the same manner each time. Begging and gaping responses to a finger can also be elicited. Once a bird has gaped, a finger poked into his mouth causes swallowing action and a slight chewing action just as in the instances when food is offered.

The swallowing action of young Blue Jays includes two or three jerks of the head back and forth as the bird gapes and the food is shoved into its throat. The nictitating membranes are not usually closed at the time of feeding, but the eyelids and nictitating membranes may be opened and closed several times in the swallowing action immediately afterward.

Placing a morsel of meat on the end of the bill of a stuffed Blue Jay and then shoving the head of this mount at the fledglings produces a strong begging reaction. (Young Mexican Jays and Steller's Jays also accept food empaled on the bill of a stuffed Blue Jay.) The nestlings will occasionally accept food using this method of presentation when they will not respond to any other method.

The first sign that self-feeding actions are soon to appear in young Blue Jays comes at an approximate age of 29 days. A young jay first clutches the perch tightly and hammers on it between his toes with the bill, in a manner similar to that employed by adult jays in feeding. Such actions have been classed as "play" in young jays by Rand (1937:38); the behavior is the primordium of a specialized motor action, general in nature at its earliest manifestation and seemingly useless (hence "play"), but it soon becomes functional. Before it becomes valuable in feeding it awaits the development of the ability to hold an object between the toes. With the first indication of self-feeding, it is almost as if an imaginary object were present between the toes. Other indications of foodhandling also appear soon afterward. One of these is manipulation of the food presented by hand to the birds. Particularly if feeding is delayed for a long time, the first few mouthfuls taken by the birds are hur-

riedly consumed as in the earlier stages of development. But subsequent offerings soon afterward are accepted in small bits from the forceps and are taken with the bill closed or nearly closed. These daintily-taken bits of food are then placed along the perch or in crevices and then "worried" for several seconds before being devoured.

When I first noticed one of my captives hammering at its perch, I placed a peanut under the bird's claws. The bird made surprisingly strong attempts to peck the nut but only got particles from it so long as I held the morsel carefully with my fingers. When I withdrew the fingers, the bird was unable to grasp and hold the nut properly and eventually dropped it. It is not until this holding ability is mastered by the bird that it is able to utilize its hammering ability to feed by itself. Particles of food taken from the forceps and placed in a crevice or merely balanced on the perch at first never are handled with the feet but only with the bill. Thus, three different indications of self-feeding appear independently and only later are perfected and then functionally co-ordinated. These three indications are (1) absence of gaping and taking food in small particles, (2) hammering on the perch with the bill, and (3) grasping and holding objects with the feet. The latter ability is the last to mature, and the functional employment of the other two must await the maturation of the third.

By approximate age 36 days, Blue Jays pick up in their bills sunflower seeds, peanuts, and other food particles and carry them to a perch where they attempt to eat them. Only with soft foods do the birds completely succeed in self-feeding. Flexible pieces of food are most often held in the bill and thoroughly whipped against the perch much as a bird does when it is attempting to kill prey such as an insect larva. The meat is then laid on a perch and pulled apart or placed in a crevice and carefully pecked.

By approximate age 39 days, the jays have become adept at holding and breaking open the shells of peanuts and sunflower seeds but still remain awkward at getting food from these. By now, the force with which they hammer the food particles is much greater. The birds also possess greater ability to hold with the feet.

Rand (1937:54-6) has written concerning the use of the tongue in manipulation of food by young Blue Jays. My observations agree with his; in preparing to eat a food object, a bird utilizes the tongue with great dexterity to roll the morsel out to the end of its bill and to retrieve the food again into the throat.

Correlated with maturation of self-feeding is the tendency of young Blue Jays to store food and other articles. The storing behavior is seemingly stimulated by (1) satiation and (2) inability to break or ingest a foreign object mistaken for food. Rand (1937:44) classified objects such as buttons as playthings, but judging from the manipulatory efforts of the jays, I think the birds regard these objects as not different from foods, such as hard-shelled nuts, that are difficult or impossible for them to open. Both food and nonfood articles are approached and handled in the same way.

I did not observe as did Rand (1937:41) the ingesting of pebbles, soil, or other foreign objects. The methods of feeding utilized on live insects by young jays are as Rand described. The birds attack the heads or other vital areas of the insects and peck at these until the insects are lifeless or the head or some other structure is pulled off.

Reaction to water.—Drinking and bathing reactions appear at about the same time. Rand (1937:35) noted that at age 19 days a young Blue Jay jumped into a container of water and paid no attention to it, but at age 25 days the bird drank voluntarily, and on the 28th day it bathed. The delay in these reactions that my young jays exhibited was doubtless due to the fact that I began giving them water with an eyedropper soon after taking them captive and did not offer them a place to bathe until after approximate age 35 days. When first they did bathe, however, the reactions were similar to those observed by Rand.

First bathing behavior appeared at approximate age 40 days. This bathing reaction follows drinking behavior. The bird drinks, then hops into the water, flutters tentatively and quickly jumps out. The jay may repeat this initial and weak bathing attempt two to three times in the next few minutes. If another young jay is present, it will watch intently the bathing attempts of its companion and may itself be stimulated to bathe. Young jays usually cease bathing if a human appears nearby. I do not know why the birds react in this way, but it might explain my failure to observe bathing by one of my captives until it was approximately 56 days of age. After bathing, young Blue Jays preen and fluff vigorously. Bathing becomes frequent and more prolonged subsequent to the initial attempt, occurring at least once a day.

Preening, bill-wiping, and head-scratching.—Preening is part of the response to wetting and certain related stimuli involving excessive moisture. Preening by young Blue Jays is, thus, always en-

gaged in after bathing takes place and nearly always when it is raining, when there is a heavy overcast, or when the humidity is high. This is true even though the birds may be inside, completely sheltered from precipitation. Preening is in addition functional in cleaning away sheaths from growing feathers as Rand (1937:53) noted. Preening behavior occurs occassionally after feeding or other intense activity that does not necessarily cause plumage to become deranged, and in these instances may be displacement activity.

True preening—activities of plumage arrangement with the bill, beyond mere picking at the feathers or the flesh beneath—of young Blue Jays is highly developed from about the time that flight feathers are half grown and the birds begin to make their initial flights (15 to 22 days). Specialized forms of plumage arrangement, such as running the vanes of remiges between the mandibles with the tip of the bill, are frequent activities of Blue and Steller's Jays, but not of Mexican Jays (see page 83). Besides preening, the Blue Jays also engage in vigorous shuffling of wings and tail, stretching of the wings, scratching of the head with a foot, and bill-wiping.

While preening arranges the barbs of each feather and assists in clearing feathers of basal sheaths, stretching movements assist in arranging the feathers properly in relationship to each other. Both activities are common to many other passerines. Swallows and Robins (*Turdus*), for example, are frequent plumage "shufflers."

Bill-wiping first appears in captive Blue Jays on the fifteenth day according to Rand (1937:53); this is in general agreement with my observations, although I found that the action becomes much more prevalent with the advent of self-feeding. Adults of all species of jays that I have observed engage in bill-wiping frequently. Although it doubtless serves to rid the mandibles and nearby feathers of excess particles or juices of foods, the action is ritualized, since it is indulged in even when seemingly unnecessary.

Blue Jays utilize the indirect method of head-scratching (the foot being extended over the top of the wing) as opposed to the direct method (*cf.* Simmons, 1957:178-9). Simmons states that a given species always utilizes only one of the methods of head-scratching, but Dilger (*in* Ficken and Ficken, 1958:277) observed a nestling Blue Jay to scratch directly, and other passerines are known to pass through brief, developmental stages of direct head-scratching. Rand (1937:53) and I observed only indirect head-scratching in captive young Blue Jays. I did not note the age at which head-scratching begins, but Rand (1937:53) recorded it

first at age 15 days. Head-scratching and rubbing the head on the perch becomes more frequent at the time of postjuvenal molt, which is heavy on the lores and circumorbital regions in Blue Jays, apparently causing irritation. Rand (1937:53-4) correlated head-rubbing with time of leaving the nest, since both occurred at the age of 19 days, but the correlation, aside from a relationship of time and maturation, seems to be invalid; there seems to be no logical reason why head-rubbing and time of leaving the nest should be directly related.

Vocalizations.—Among the young of species under consideration herein, Blue Jays exhibit by far the largest variety of call notes. (Adult Blue Jays are similar in this respect in comparison to adults of the other species.)

Newly hatched Blue Jays utter a high-pitched squealing call, *squee, squee,* when the nest is touched. This call is not harsh in quality but is penetrating at short range. By the end of the first week of life, this squeal has a harsh quality, *squrreesh,* and the volume of the call is greater. Both of the above calls are food-soliciting calls given only when the nest is moved slightly as the adults land on it, or when food, an object even vaguely resembling food, or the bills of the parents are directed toward the young birds. For at least the first ten days, no other calls are given regularly except an occasional peeping note, which seems to indicate satisfaction or satiation after feeding.

From the middle to late nestling life, a rich chortling call is added. It is given at the moment that food is received and is continuous with the *squreesh* call, hence: *squreesh-oritch-oritch-oritch.* In addition, a series of twittering notes, *peter peet-peeter* is uttered after the food has been swallowed. A suppressed version of the squealing or whining note given before food is taken is sometimes uttered after food is swallowed. Water presented to the birds evokes the same calls as does food.

The calls described above are retained in post-nestling life as important parts of the repertoire of the birds. Wild juveniles flying about the trees in June and July in Kansas utilize exactly the same calls.

With the advent of postjuvenal molt, there are additions to the repertoire of calls and changes in quality of calls already possessed. Soliciting, chortling calls, and calls of satisfaction gradually drop out of use with decreased dependence for food upon adult jays or humans.

Additional calls appearing in the repertoire include a variety of

faint "conversational" notes and a remarkably varied song, given by both sexes. The conversational notes are usually given by two birds at the same time and consist of a nearly steady stream of twitterings, soft chirping notes, and a stuttering, whining call. The song of these birds is their noteworthy vocalization; I did not hear it given by young Mexican or Steller's Jays. The song is definitely closely related to the conversational notes. While the latter are often given at times of great activity, the song is given only when such activity ceases. The conversational notes often lead gradually into singing; the twitterings and chirpings become more intense and closer together and finally form a rich many-syllabled song. This song is somewhat like those of the Purple Finch (*Carpodacus purpureus*) and the Blue Grosbeak (*Guiraca caerulea*) but harsher and more uneven in rendition. The song is given *sotto voce*, seemingly indicating contentedness, rather then being given as an announcement of territoriality. (Adult Blue Jays occasionally engage in such singing in the wild.) Another call, *chur chur*, is rarely given by young Blue Jays and is uttered at times of fright.

From late in the postjuvenal molt on, the development of adult calls gradually takes place. These include only variations of the *jay* call (of assembly and alarm) at least up to approximately 118 days of age. No indication of the pumphandle or squeaky-gate calls (associated with courtship and suppressed aggression) or other calls of the adults are given in this time; it is probable that these more specialized calls are not given until at least the autumn of the first year of life. The *jay* call given by these young birds is derived from the *squrreesh* of begging juveniles and is more nasal in quality than the *jay* calls of adults, although it is uttered under similar conditions. Begging juveniles flying about in late summer and early autumn can be heard giving calls intermediate between these two calls.

Finally, there is a harsh *cuz cuz* call, which young Blue Jays give only rarely, each time after feeding. It is associated with restless behavior occasionally exhibited just after the last of a supply of food is devoured and before the birds settle down to rest.

Relationships with one another and other birds.—Young Blue Jays seldom quarrel with each other, as Rand (1937:56) observed. Nestmates, in fact, engage in almost all of their activities together, only rarely struggling with each other over morsels of food. Fre-

quently, they do pull at opposite ends of pieces of paper or steal peanuts or pieces of bread from one another, but there is never any resulting threat from the loser after these interactions.

If a Steller's Jay or a Mexican Jay of approximately the same age as young Blue Jays is placed in their cage, they proceed to become acquainted with the stranger by a ritualized method. The Blue Jay approaches and with the bill pulls at the feathers in the alular region of the other bird. Then the Blue Jay pulls gently at the toes, rectrices, nape feathers, and circumorbital feathers of the stranger; the latter remains nearly still during the investigation. The pulling and pecking is never vicious. Young Blue Jays occasionally administer such treatment to each other, but less intently. I am not certain of the significance of this behavior, but it is correlated with the habit of juvenal Blue Jays of investigating *all* strange objects, animate or inanimate, by lightly pecking or pulling at them. The behavior has a counterpart in aggression of the peck-order in the Mexican Jay (Fig. 19).

At approximate age 35 days, the first evidence of the habit of the male of feeding the female appears in Blue Jays. When a young male holds a piece of food in his bill, a young female may beg him with bill open and wings quivering. Rand (1937:56) noted begging of one young jay by another but found that it always elicited a similar begging response from the other bird. Such behavior is more difficult to relate to courtship feeding behavior. However, in my two birds, the begging by the female usually stimulated the male to feed her or at least go through the motions of feeding her. Such behavior would seem to indicate a close relationship of courtship feeding and feeding of young birds by adults. Only once did I see the male solicit food from the female. The latter did not possess food at that time and did not respond to the behavior of the male.

Relationships with enemies.—When mounted specimens of the Sharp-shinned Hawk (*Accipiter striatus*) or the Long-eared Owl (*Asio otus*) are brought in sight of a young Blue Jay, it reacts by lowering its crest, crouching, and eyeing the object with one eye. When the mount is brought close to the bird, it flies about in wild panic, uttering no calls. The reaction toward the mount of the hawk is less intense than that toward the owl. When a stuffed Blue Jay is presented to juvenal Blue Jays soon after the presentation of the specimens of predators, it evokes no reaction. Neither Blue Jay in this study had ever seen a live hawk or owl.

The birds also react toward predators such as coatimundis

(*Nasua narica*), several of which came near an outdoor cage containing my captives. But in their response to these mammals, the birds were highly vocal as they flew about in the cage, giving a loud whining call that I otherwise never heard them use.

Relationships with humans.—Young Blue Jays can be treated in such a way that they regard humans as their fellows. I successfully discouraged such behavior in the captives as mentioned earlier. Though the birds did not fear me if I sat in the room and watched them or fed them, they were frightened if I attempted to handle them. The only threat reaction they ever exhibited was toward me, and this occurred only when I poked at them in a deliberate attempt to provoke such a reaction. In threat reaction, the crest is raised and the mouth opened toward the aggressor; the body is held erect and no calls are given. The jays had no opportunity to become familiar with other humans.

Sleeping.—In the daytime, a young Blue Jay frequently dozes with its bill directed forward, but at night it always sleeps with its head turned posteriorly and its bill inserted among the feathers of its back. In either case, the two feet of the bird clasp the perch and the body is lowered to a crouched position on the tarsi. As the bird grows older, it crouches less while sleeping. Rand's (1937: 52) observations on sleeping of young Blue Jays agree with mine on the preceding points. Rand states that the young do not tuck their bills in the back feathers in sleeping prior to age 20 days, which in the wild would be the period when the young were in the nest and when adult roosting habits are not developed.

Young Blue Jays are easily aroused from sleep and immediately become active in such instances. When allowed to awaken naturally with the coming of daylight, they do so at dawn but do not become active until they are fed, whereupon they may undertake intense excited movements about their confines.

Diurnal sleeping decreases gradually and simultaneously with the development of independent feeding, flying ability, and other signs of maturation. Sleeping in daylight hours disappears entirely as the postjuvenal molt progresses.

Behavior of a Young Steller's Jay in Captivity

I raised a young Steller's Jay from the late nestling stage (approximate age 15 to 20 days) through the greater part of the postjuvenal molt (approximate age 120 to 125 days). Until approximate age 50 to 55 days the bird was kept in a cage by itself part of the time and in a cage with two young Blue Jays part of the time.

It was frequently kept in the same room with young Mexican Jays in this period. When the bird was able to feed for itself, it was transferred to a large outdoor cage containing a young Blue Jay and a young Mexican Jay of maturity similar to the Steller's Jay.

In the development of flying ability, feeding and drinking methods, manipulatory ability, preening, vocalizations, relationship with other animals, and sleeping habits, young Steller's Jays are remarkably like young Blue Jays. Minor differences between the two species in these aspects of behavior were probably due to the greater reticence of the Steller's Jay, at least until the time of late postjuvenal molt. This greater reticence may have been caused by the lack of competition and companionship from another young bird of the same species. At postjuvenal molt the two species of *Cyanocitta* diverge in behavior most notably in vocalizations. As indicated above, their juvenal calls are similar, but with maturation young of each species begin to acquire calls characteristic of adults of their species.

Behavior of Young Mexican Jays in Captivity

Two young Mexican Jays were raised in this study. One was taken from the nest at approximate age 25 days (its nestmates had already flown). The other was captured when still unable to fly strongly at approximate age 28 days. The two birds were retained in captivity until approximate age 60 and 116 days, respectively. The birds were given care and treatment similar to that given young Blue and Steller's Jays. I was not able to tame the two Mexican Jays so well as young of *Cyanocitta* so that behavior of the former for the most part was probably not typical of young of that species in the wild.

Young Mexican Jays are similar to young Blue and Steller's Jays in their behavior patterns and in the development of these patterns. Mexican Jays differ from *Cyanocitta* behaviorally in the following ways.

The use of the tongue in feeding and other manipulatory activities is not well-developed.

Young Mexican Jays do not drink as much water as do young Blue Jays and probably Steller's Jays, although independent drinking ability appears at about the same time in all three species. It is possible that the failure of young Mexican Jays to drink as much water as the others is correlated with the fact that the Mexican Jay lives in a more nearly arid climate. My captive young

Mexican Jays did not bathe, either, which might be correlated with the occurrence of the species in arid regions.

In additon to drinking little and not bathing, young Mexican Jays do not preen themselves dry when their plumage is thoroughly wet down in the laboratory. Young Blue Jays and Steller's Jays treated similarly preen vigorously. The preening habit is not totally absent in Mexican Jays, since the adults preen, although they do not do so as often as do Blue and Steller's Jays. Young Mexican Jays do fluff their plumage in attempts to rearrange the feathers. I know of no published information concerning development of the preening habit in birds. I assume that most birds preen after becoming wet, but possibly those living in drier climates have less well-developed preening habits. Preening, after all, hastens drying, which would hardly seem conducive to the conservation of moisture, which is managed by most organisms inhabiting arid climates. Of importance to individual birds, of course, is the function of water on the plumage as an "evaporative cooler" in arid places immediately after a rain. Failure of the birds to preen also would prolong the effects of this cooling system.

The vocal repertoire of young Mexican Jays is of lesser variety than that of young Blue or Steller's Jays. There is no song (in young or adults). The begging call in early nestling life is a high-pitched whistle, *shreee*, becoming *choreee* in later nestling life, with an appended *itch-eeitch* as food is accepted. In post-nestling life one additional begging call, similar to the begging call of young Starlings, is added to the repertoire. The adult conversational notes, *kwot kwot* or *whut whut*, and the alarm and assembly calls, *reek reek*, are a part of the repertoire prior to postjuvenal molt, in contrast to the failure of adult *jay* calls to appear in Blue Jays until postjuvenal molt stage of maturation. Moreover, whereas the *jay* calls of young Blue Jays are easily distinguishable from *jay* calls of adult Blue Jays, the *reek* calls of young Mexican Jays are like those of the adults.

Juvenal Mexican Jays exhibited little fear response toward a stuffed Long-eared Owl that frightened juvenal Blue Jays nearby. Since adult Mexican Jays in the wild mobbed this same mount, either captivity altered the natural behavior of the young Mexican Jays or fear of predators in the species is learned. However, because of the unusual lack of fear exhibited by adult Scrub Jays in the wild toward mounts of predators, it seems well to mention this similar behavior of the young Mexican Jays.

FLOCKING AND FORAGING BEHAVIOR

Jays are generally gregarious. They are not secretive as individuals or pairs, although territoriality exists in some species as we have seen. Size and kind of groups vary considerably in different species of jays, even within the same genus. Blue Jays and Steller's Jays gather in flocks in the nonbreeding season. In the former species, these flocks vary in size from five to fifty or more birds, and the aggregations are loosely organized. One seldom sees 20 Blue Jays fly as a group from one tree to another as frequently is observed in Mexican Jays. Unlike the latter species, there seems to be a weak tendency toward unison movements of Blue Jays and toward much interaction of any sort between members of the flock; the birds move and feed singly; there is much leaving and re-entering of the flock by individuals. Steller's Jays form flocks less frequently than do Blue Jays, but the aggregations are of the same degree of organization. The genus *Aphelocoma*, however, exhibits at least two degrees of organization of the flock. Whereas the group is maintained by such a strong bond in Mexican Jays that unison movements in any season (as well as semi-communal nesting) are characteristic, Scrub Jays have a less well-developed flocking tendency, perhaps less than any other species in either *Cyanocitta* or *Aphelocoma*.

Flocking, Movements and Foraging in the Blue Jay

Autumnal flocking.—Loose aggregations and the independence of individuals are characteristic features of flocks of Blue Jays in autumn. A flock of 50 of these birds in an open oak-hickory grove may center its activity in one or several large trees, usually those containing a supply of acorns, upon which the jays feed. Jays in these flocks are not noisy but limit their vocalizations to occasional, low-intensity *jay* calls and the *wheedle-eee* call. There is a steady but loose stream of birds leaving and entering the trees. Many of the birds take acorns from the tree, remove the husks, and carry them one to three at a time away from the grove. Birds returning presumably have carried acorns away to some distant hiding place. Some members of the flock fly to the ground and bury acorns in the soft earth. A few birds feed on the fruits in the tree, while still others store acorns in crevices high in branches of the trees.

Direct relationship between individuals in these fall flocks is fairly common but always involves aggression. This is wholly threat, since there is no real conflict or contact between the birds. Usually such interactions concern a food article. One bird may

store an acorn immediately after which another jay, having watched the storing procedure, may take the acorn and flee with it. The first bird, if it is still nearby, may then give chase briefly. Each Blue Jay seems also to carry with him a foraging "territory" to which the term "individual distance" (*cf.* Hinde, 1956:342) is applicable. When another jay approaches to within a few feet, it is usually chased away to a distance of 20 or 30 feet before normal foraging by both birds continues. If the flock is large and all its members are feeding in the same tree, the size of these "portable territories" is smaller; their boundaries often are trespassed, so that frequent, short chases and skirmishes occur. Aggression is not accompanied by vocalization for the most part. The antisocial tendency of each jay is evidence of the type of flock characteristic of the species in autumn.

In autumnal flocks of Blue Jays, reactions toward individuals of other species of animals occasionally occur. In fact, when a predator is discovered the group of birds may become a closely knit organization in expression of mobbing behavior.

Postbreeding flocks begin to form late in summer and are composed of several family groups of an area. As was discussed earlier, feeding of young jays by the parent birds continues for several weeks, perhaps occasionally for well over a month after the young leave the nest. In this period, the young and adults commonly move over an area several times the size of the territory, an area comparable to the home range of the parental birds. By early August, this range is expanded still more, and three or four family groups eventually begin to concentrate their movements in the most favorable place where their home ranges overlap. In this way, a loose flock begins to form.

These family groups largely maintain their discreetness in late July and August, moving within the same grove, often occupying the same tree. At this time, the young are easily distinguishable by their juvenal plumage and their habit of frequently begging the adults for food. This disbandment of family ties is closely correlated with the onset of the postjuvenal molt, as indicated previously. This molt begins in middle or late July for some birds that fledged early, but it is not well under way for most of the young in the region including Kansas until August. Young that were dependent upon parents for food acquire independent feeding abilities at the time of this molt. But in spite of the disappearance of family ties, the birds continue to frequent the area resulting in the loose flocks of autumn.

Large flocks of Blue Jays are maintained generally from September until late November or early December; a diminution in size of the aggregations accompanies the first extended cold period of winter.

Blue Jays also flock in autumnal migration. I have little first-hand evidence on the composition of these flocks, since they are usually observed flying high overhead, where their members can neither be aged nor shot. In October, migrating groups of from 15 to 50 Blue Jays are frequently noted near Lawrence; they fly in straggling formation and sometimes land in the tops of large trees. It is characteristic of these migrating birds that they are silent or nearly so, in contrast to courtship flocks of jays in the spring. Adult Blue Jays in eastern Kansas may be nonmigratory, and first-year birds may be entirely migratory; data concerning this are discussed under winter flocking.

Winter flocking.—Typically in winter, one finds groups of two to four Blue Jays, but seldom large flocks. These small associations are evenly distributed over an area with the birds occupying winter ranges that may be "defended." Continued observation in a given area reveals a small and constant number of individuals to be present. If members of a resident group are trapped and removed or shot, they will be replaced by other jays so that the area continues to support the same number of jays through the winter. At least this is true if the area is particularly favorable—containing abundant food and shelter. Probably jays replacing those removed come to the area from a less favorable winter range.

Pitelka (1946:82-4) suggested on the basis of his own investigation and those of other workers that subadult Blue Jays may be migratory, though perhaps only in the northern states. He further suggested that adult birds may gradually become sedentary. Of specimens that he examined in the Museum of Comparative Zoology, 29 first-year birds were collected north of the Mason-Dixon Line, and only four of these were taken in December, January, and February. First-year Blue Jays can be distinguished with experience and practice by their tapered rectrices and dull-colored outer primary coverts and alulae (*cf.* Pitelka, 1948:83). Laskey's (1958: 211-18) banding studies indicated that first-year birds leave the area of Nashville, Tennessee, in their first winter and that the wintering grounds of these birds range from Alabama to Mississippi.

According to results of my trapping and specimens in the collection of the University of Kansas, wintering Blue Jays in Kansas

are almost all adult birds, whereas beginning in April and May and continuing through September, the numbers of subadult birds equal or surpass the numbers of adults (Fig. 18). Since fall migration of Blue Jays in Kansas occurs in late September and October, birds present in Kansas in November are mostly wintering individuals. It is probable, then, that first-year birds are the principal migrants of the population in Kansas. The resident Blue Jays in Kansas in winter begin courting in late February, and daily observations indicate that wintering birds seen courting then are the ones that begin nesting in the same area a month and a half later.

Analysis of specimens of Blue Jays taken throughout the year in the lower peninsula of Michigan indicate that there, too, adults constitute the greater portion of the population outside the breeding season, while the proportion of adults to subadults is approximately equal in the summer months, June through August (Fig. 18).

One would logically suspect that in winter in the southern states subadults would far outnumber adults, assuming that the populations of Blue Jays breeding there are more sedentary than in the north, and that the incoming migrants are principally subadult birds. However, analysis of 92 specimens taken in Louisiana and Mississippi indicate that there, at least, no such ratio of subadults to adults is created (Fig. 18). Several possible reasons may explain this fact, as follows: (1) The collection from Louisiana and Mississippi contains more adults, because these are easier to kill (data from the collections made in Michigan and Kansas tend to refute this assumption); (2) subadult birds do not migrate south (but these age groups from Michigan and Kansas must go somewhere in winter, and observations in spring and fall indicate south to north and north to south movements of Blue Jays); (3) subadult birds from the north either spread out over a large area, winter in the southern states but not in or so far south as Louisiana and Mississippi (Laskey's, 1958:215, data contradict this), or disperse over a large area in the south so that a change in age-ratio at a given place or in a given small sample is hardly detectable.

The last possibility seems to me to be the most logical; it is evident that birds summer resident, for example, at Nashville, Tennessee, disperse over a wide area in winter, including Alabama and Mississippi (Laskey, 1958:215). Probably birds nesting in Kansas and Michigan do not also migrate in large numbers this far south but replace in winter the summer resident population of Tennessee, Kentucky, and Arkansas. The problem might be easier to inves-

tigate if each individual specimen from the southern states in winter were determinable to subspecies (either *bromia*, migrants from the north, or *cristata*, the resident birds). But a broad cline in mensural characteristics exists between the two "subspecies," making racial determinations of individuals hazardous where interspersion of the birds occurs in winter.

Food-storing.—Food-storing is a well-developed habit in the Blue Jay. It seems that sometimes the behavior is not functional in assuring a food reserve, since an occasional jay will carry a small particle of food high into a tree and wedge it into a crevice between a bud and a twig, where the morsel could not possibly stay following the first strong wind. Furthermore, storing may take place in spring when food is plentiful. In addition, jays many times store small bits of food and minutes or seconds later return, extract, and eat the particles. They may take into their mouths and gullets more than they can possibly eat at once when they are confronted with a large supply of food. But they will carry off such surpluses, disgorge the morsels piece by piece, sticking one in one crevice, another some other place, and so on until each piece is stored or eaten. Usually these stores will not be touched again and thus go to waste, judging by observations of captive birds. The latter would seem to have a better chance of remembering or accidentally coming upon their stored food supplies than do birds in the wild. It is certain that in the wild, the type of place often chosen for storage is not easily marked or remembered by the birds. I have mentioned already that stored food may be taken immediately by a jay other than the one that stores it; this is particularly true in captive birds.

It is difficult to believe that the habit of storing food has arisen in jays in direct response to a need for a future supply of food. Possibly there is conflict between stimulus to eat provided by the presence of food and stimulus to discard the food caused by the lack of physiological need for sustenance, and this results in displacement storing. Perhaps, on the other hand a more involved, less direct explanation is necessary—that food-storing is an expression of winter territoriality. Food-storing as a possible spacing mechanism in a winter population of a species previously seems not to have been discussed in the literature. Lack (1954:256-7) discusses winter territoriality in birds, pointing out that in some species it seems functionless, in others it may ensure ownership of the area in spring, and that in others there is a suggestion that there

is food value. But under the latter factor, he mentions only actual feeding (not storing) and involves food in territoriality as a reason for spacing, not as a means of it.

As an example of how this mechanism might function, we may imagine that a supply of seeds is suddenly made available within the wintering area of several Blue Jays. This supply is more than can be eaten at once, yet another similar supply might be unavailable for weeks. If the resident Blue Jays eat only what they immediately need, they leave "in circulation" an amount of food that if found by intruding jays might encourage the latter to frequent that area regularly, not only when surplus food is available, but more important, when it is not. The resident jays by taking out of circulation not only the immediately devoured seeds but also those that are soon stored (making them comparatively unavailable, at least) may not ensure a future food supply composed of these stored foods, but may ensure their acquisition of future foods that appear in the area, by having discouraged intruding jays from remaining or from returning. If, of course, the increased food supply is such that the resident jays of the area cannot keep all of it out of circulation, then the carrying capacity of the area is actually increased, and the number of resident Blue Jays can naturally increase.

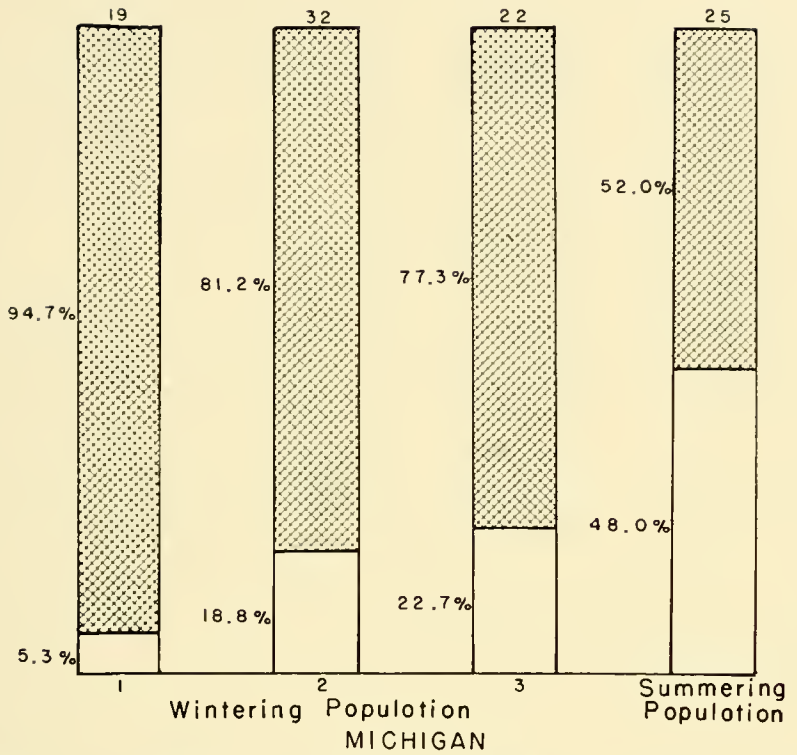
Flocking, Movements, and Foraging in the Mexican Jay

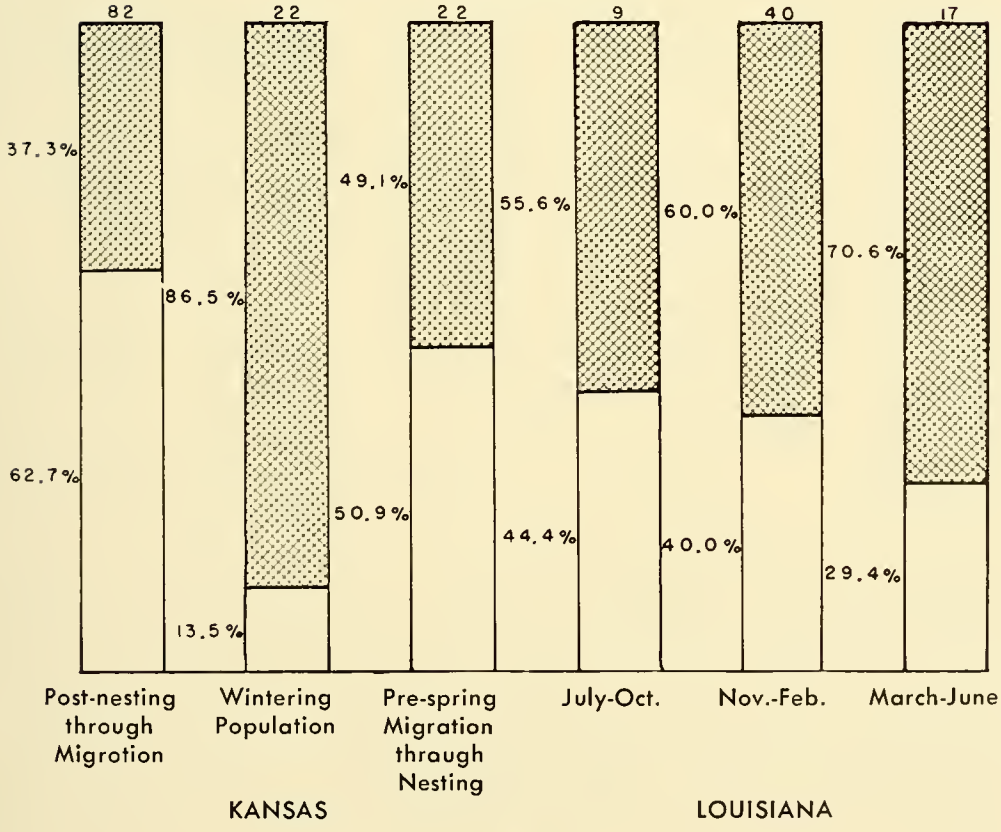
I have not had the opportunity to observe flocking behavior in this species in autumn and winter, but presume it to be similar to flocking in early spring and after nesting is completed in late summer. What I have previously said concerning flocking at the time of nestbuilding and during feeding of the young that have left the nest points out the basic differences between the flocking habits of this species and jays of the genus *Cyanocitta*.

Flocks of the Mexican Jay are highly integrated aggregations in which the individual members all move, feed, rest, sleep, mob, and in other ways act alike as a unit. Flocks are probably in all cases family groups that remain together throughout the year, if, again, we may judge from flocks of early spring and late summer. No migration occurs, but the flocks wander to lowland areas occasionally.

Activities of the flock.—Except in the nesting season, flocks of Mexican Jays wander about the low hillsides, foraging along creek-bottomlands, in groves of oaks, or in the scrubby vegetation con-

FIG. 18.—Relative abundance of adult and subadult Blue Jays in the lower peninsula of Michigan, Kansas, and Louisiana-Mississippi based on specimens in the collections of the University of Michigan, University of Kansas, and Louisiana State University, respectively. In the Michigan section, the first three columns represent (1) September-October, (2) November-February, (3) March-May. The wintering period there is divided to illustrate the lack of significant changes in the composition of the population taking place from September through May. In the section concerning Kansas, the divisions seem self-explanatory. In the section concerning Louisiana, the divisions are arbitrary, since no significant changes in the composition of the population were evident. Crosshatched areas of the columns represent the percentage of the samples composed of adult Blue Jays. Clear areas of the columns represent the percentage of the samples composed of first-year Blue Jays. The actual percentage indicated in each portion of each column is given numerically to the left of the portion of the column to which it refers. The numeral above the top of each column indicates the number of specimens composing the sample.


19
32
22
25
94.7%
81.2%
77.3%
52.0%
48.0%
22.7%
18.8%
5.3%
1
2
3
Wintering Population
Summering Population
MICHIGAN


82
22
22
9
40
17
37.3%
86.5%
49.1%
55.6%
60.0%
70.6%
62.7%
50.9%
44.4%
40.0%
29.4%
13.5%
Post-nesting through Migrotion
Wintering Population
Pre-spring Migration thraugh Nesting
July-Oct.
Nov.-Feb.
March-June
KANSAS
LOUISIANA

sisting of scrub oaks, pinyons, junipers, and herbs. The flocks are difficult for an observer or predator to approach without being detected, because all members are wary and ready to give the alarm cry, setting the entire group to flight. Particularly when the flock is feeding in open vegetation where individual birds are easily seen on the ground, one or two members may remain on exposed perches above the flock—seemingly serving as lookouts. The location of a flock of Mexican Jays may be detected by the presence of these lookouts scattered about a hillside.

Although most feeding by a flock is on the ground or in low vegetation, occasionally in early morning hours, aerial feeding may be indulged in by Mexican Jays. In this activity, the jays sit on exposed perches and launch themselves flycatcher-like after passing insects, catch them, and return to their perches. Though not as quick and adept at the process as true flycatchers, the jays nevertheless are successful at foraging in this manner. I have never observed other species here treated to feed in such a manner. Characteristically, most or all the members of the flock engage in flycatching at once.

Flycatching by the flock seems to accompany another frequent habit—sunning, in which the birds of the flock sit scattered about in the tops of low trees on exposed hillsides for periods up to an hour in length. Sunning is always engaged in at the time when the sun first appears over the hills, and seems to be most frequent in cool weather. A sunning bird sits facing the sun, with plumage fluffed, and neck drawn in, almost as if going to roost.

Sunning time is a period of rest for the jays. It is not, however, the only diurnal rest period. On a clear day there is at least one other period of rest, which usually comes around noon. In inclement weather, much of the afternoon may be spent by the flock, sitting in dense low trees in sheltered places. In early April when the temperature is near 40° F, one may find flocks of jays in the afternoon sitting quietly in oak scrub among boulders at the bases of cliffs or in other nooks protected from the weather. In such situations, a flock is difficult to excite, and the presence of a person merely causes the birds to call briefly and move only far enough to be away from the observer, where again the birds become quiet.

Though I have never been able to discover a roosting flock, I have followed groups until nearly dark and presumed that they roosted in trees along gullies on hillsides. In my experience, the birds do not cease activity in the evenings or resume them in the morning along the canyon floors but always on the hillsides.

The typical daily routine of a flock of Mexican Jays seems to consist of a regular sequence of events occurring at specific times. Activity of the flock begins about one-half hour after dawn at which time the birds can be heard calling from the hillsides. There is then a brief period of movement in which the birds fly to their regular sunning locale, which for each flock is fairly constant and is an exposed place on an eastwardly facing hillside. Here the birds become quiet and sit about in the low trees, where they remain, with limited movement and feeding, while the sun rises. The birds stay at this place until the sun has been up from one-half hour to a full hour before they begin to forage actively. By 9:00 a. m. the flock is in full activity and moves down the hillside as the air warms, ultimately reaching the canyon floor. Here, the birds forage in the woodland understory and on the ground. This activity of the jays continues until between 11:00 a. m. and 1:00 p. m., whereupon a period of rest occurs, lasting one to two hours. Feeding and other activities of the flock are resumed usually by 2:00 p. m. if the day is fair and continue until 5:00 or 6:00 p. m. After this, the birds begin their movements back up the hillsides along the small ravines and gullies to their roosting places. There may be a short period of flying about in the hours of evening, usually around 6:00 p. m., at which time the flocks are conspicuous. This may be a period of reorganization of the members of the flock in preparation for the movement to the area where they will roost.

Food-storing.—Food-storing is apparently uncommon in Mexican Jays in the wild, although my captive individuals frequently stored food. I watched a flock of Mexican Jays in the Chiricahua Mountains engage for several days in carrying small green apples far up the mountain sides from an apple orchard in a canyon. But I was unable to discover what the birds did with these fruits. Some of these small apples evoked no reaction from two Mexican Jays when placed in a cage with them.

Gross (1949:241) noted that Mexican Jays in the Santa Rita Mountains of Arizona readily came to food placed on a feeding shelf near his camp. The birds were especially partial toward bread broken in large pieces. These they frequently carried off two or three at a time and stored in crevices in trees. One jay was observed to fly to the ground and cover its piece of bread with leaves.

Under normal conditions in the wild (no artificial food supply being present) it seems probable that Mexican Jays store food less

frequently than do Blue Jays. It is a common sight to observe the latter species store food, but under similar natural conditions in the wild, one seldom observes food-storing by Mexican Jays.

INTERSPECIFIC RELATIONSHIPS

Interspecific Relationships of the Blue Jay

Blue Jays are typical corvids, bold, inquisitive birds, often involved in mobbing of predators or in other strife. They are quick to lead a fight against predators, yet are themselves predators and are generally recognized as such by other species of birds.

Relationships with nonpredators.—Blue Jays quarrel most frequently with Robins (*Turdus migratorius*). The latter, in the region of Kansas, in suburban habitats nest in close proximity to the jays, often in the same trees. Robins are usually the aggressors in interactions with jays, attacking them on little provacation. The jays seem always nonaggressive toward adult Robins and barely avoid their plunging assaults.

I have not seen Blue Jays robbing nests of other species, but an acquaintance brought to me two fledgling Mourning Doves (*Zenaidura macroura*) she had rescued from attacks by two Blue Jays. The literature, of course, contains references to the habits of Blue Jays of killing young birds, devouring eggs, and indulging in other acts of predation. The frequent alarm reactions of Robins as well as Tufted Titmice (*Parus bicolor*), Brown Thrashers (*Toxostoma rufum*), Baltimore Orioles (*Icterus galbula*), and other species toward Blue Jays is further evidence of the status of this species in the avian community.

Relationships with predators.—The arousal of mobbing behavior in the Blue Jay varies considerably in procedure. Often, it develops in stages, each having an associated posture or display and vocalization. The initial stage is often one of curiosity (marked by erect, investigatory posture, Fig. 4, and the *kut kut* or *kuet kuet* call). This may be followed by anxious uncertainty (*bobbing* display with the *wheedle-eee* call), developing quickly to the stage of "identification" of the predator (*bobbing* with the *cleeop* call). "Identification" leads to "realization" of danger (aggressive and intense investigatory postures and displays with the *jayer* and *jaay* calls, the latter associated with greater excitement than the first). The jay then sounds the call of alarm (*jaay, jaay, jaay,* given repeatedly), whereupon a group of jays assembles within minutes. Mobbing

then takes place, the birds diving at the predator, giving the *jeer jeer* call, and engaging in *bobbing* display.

Blue Jays mob in groups of three to 12 individuals. Mobbing behavior is characterized by an aggregation of aroused jays dispersed at distances of 20 to 50 feet from and surrounding the object of attack. The birds usually remain above the predator. If it is the nesting season, and the predator is near the nest of a pair of jays, the pair owning the nest will approach the predator much closer than do other jays. If the predator is reluctant to leave, the attack may reach a point where the two jays dive at the enemy. In my experiments using a stuffed Long-eared Owl and a stuffed Sharp-shinned Hawk, jays always struck the specimens several sharp blows on the nape, in the course of mobbing, but usually made passes to within a few inches of the heads of the mounts.

In such attacks, a jay moves to a place above the predator and within approximately ten feet of it. From here the jay drops silently, pulls up just short of the predator, and rises to a safe distance screaming, *jeer jeer.* Such an attack usually provokes the remainder of the mob to loud vocalization, which includes a variety of *jay* calls plus the *br'r'r'r'r'* call and, less frequently, the *cleeop* and *wheedleeee* calls. The several calls uttered indicate the variety of responses exhibited toward the predator.

The increased excitement that occurs when a jay attacks is at least in part due to the resulting movement of the head and body of the predator as it avoids the jay. If the predator remains completely motionless, as was the case with the stuffed specimens (except when the wind caused motion) the intensity of the mobbing reaction will eventually regress. Blue Jays can become conditioned to the stuffed specimens; although the birds will always show initial concern when confronted by mounted predators, the excitement subsides more quickly each time the jays are subjected to the artificial stimulus.

When a predator flees, Blue Jays follow but do not mob in the air. If a predator alights only a short distance away, the jays continue to mob it. If, however, the predator flies high or leaves the woodland where the mobbing is occurring, the attackers do not follow, and the mobbing reaction subsides quickly. The individual jays then disperse quickly to their respective ranges.

Though displacement and redirection behavior are not well-developed phenomena in the Blue Jay, an example of each is occasionally seen at the time of mobbing. Displacement bill-wiping

(the autochthonous pattern follows feeding and, sometimes, preening) is undoubtedly indicative of conflict between tendencies to attack and flee. In this behavior, the bird quickly wipes the sides of the bill back and forth several times on the limb or other perch on which he stands. Redirection behavior in the presence of a predator occasionally is directed toward another jay that is not participating in the mobbing.

Most frequent victims of the Blue Jay near Lawrence are the woodland hawks (*Accipiter spp.*), and the Great Horned Owl (*Bubo virginianus*). The only mammal that I have seen Blue Jays molest is the Fox Squirrel (*Sciurus niger*), which probably is a predator at the nests of jays. Strangely enough, the reaction toward the squirrel is totally different from the reaction toward the hawks and owls. Blue Jays never mob squirrels and ignore them for the most part outside the nesting season. When a squirrel enters the vicinity of a nest of a jay, the birds fly to the animal and silently follow it. While following and literally "herding" the squirrel, the birds occasionally dive at and snap their bills at the animal, but utter no sound except low intensity *kut* or *kuet* notes. Because the attacking birds do not give alarm calls, the assembly of a mob does not occur. Blue Jays show no fear of squirrels. Occasionally they swoop upon a squirrel that is not close to their nest and harass it for no apparent reason.

In comparing the mobbing behavior of Blue Jays with those of other species of jays discussed herein, it should be emphasized that Blue Jays typically strike the predator in mobbing; this contact is forceful, terminating a dive by the attacker. In the breeding season, close approach to the predator is made usually by only two birds, the owners of a nearby nest.

Interspecific Relationships of the Mexican Jay

The Mexican Jay holds the same community status as the Blue Jay, sharing with it certain behavioral characteristics of both predator and prey.

Relationships with nonpredators.—The relationship between the Mexican Jay and the Western Wood Pewee (*Contopus richardsonii*) is similar to that between the Blue Jay and the Robin. Interaction between these two common inhabitants of western woodlands occurs only in the breeding season and seems to stem from apparent concern on the part of the flycatchers for their nests, eggs, and young.

Gross (1949:241) noted that at a feeding tray, Mexican Jays completely dominated other birds that came there except the White-winged Dove (*Zenaida asiatica*). He also observed possible predation by a flock of jays on the eggs of the Solitary Vireo (*Vireo solitarius*) and the young of the Blackheaded Grosbeak (*Pheucticus melanocephalus*). According to my observations, Mexican Jays are less antagonistic toward other species of their community than are Blue Jays. Since the Mexican Jay is intraspecifically social to a high degree, its activities less often give cause for excitement in individuals of other species.

Relationships with predators.—Mexican Jays are more easily incited to mobbing reaction than are Blue Jays. Mexican Jays also remain in an excited state for a greater period, whether or not the object of mobbing is alive, or remains to be mobbed. This greater and more prolonged excitability seems to be a function of greater sociality in the species than in the Blue Jay. The jays tend to stimulate each other to a greater degree than is possible in less social species. The high degree of sociality also ensures a larger mobbing contingent, also resulting in greater excitement.

A stuffed Long-eared Owl placed in a prominent place within the foraging range of a flock of Mexican Jays, stimulates not only the members of the nesting pair, or pairs, to mob, but the entire flock resident in the area as well. It is impossible, after mobbing begins, to distinguish between the members of a pair owning a nearby nest and the other jays engaged in mobbing. All birds mob in approximately equal degree, all come close to the predator, and all give vent to loud calls of alarm—the *reek reek* and *ruik ruik* vocalizations.

Mexican Jays show less tendency than do Blue Jays to follow a predator if it flies from one part of a woodland to another, unless the predator remains in sight and moves only short distances at a time. Nevertheless, if the predator leaves or is removed (as in the case of stuffed specimens), the jays remain where the object of mobbing *was* and continue to call. Mexican Jays also associated me with stuffed mounts of predators and frequently followed me, calling excitedly, in the several days after they had observed me carrying one of the specimens that they had been mobbing.

The only time in the nesting season when the presence of a predator seems unlikely to cause mobbing by a large number of Mexican Jays is during incubation. At this time, a stuffed specimen of a predator placed near an incubating female excites her, but may

not arouse other jays to mob, although they are in the vicinity. Other jays, in such instances, will sometimes approach to nearby trees and give an occasional *reek* call of alarm, but in my experience will not mob. I have previously stated that a female Mexican Jay that I observed in incubation was nearly deserted by the resident flock. The failure of members of this flock to mob coincides with their failure to exhibit other types of attentive behavior at the nest during incubation. At the same time, the incubating female vigorously attacked mounts of predators near the nest. In these attacks she struck the specimens. Behaving much as a Blue Jay does under similar circumstances, she perched above the predator and then dived silently to deliver a sharp jab at the nape, after which, calling loudly, she rose quickly to a safe position.

Mobbing reaction by a flock seldom seems to include contact by any jay with the predator. The jays typically perch 10 to 20 feet away from the object of mobbing and scream in alarm. *Tail-flitting* and *bobbing* are characteristic displays in mobbing by Mexican Jays. The *bobbing* action is not the exaggerated performance typical of the Blue Jay in courtship and is closer to a bowing action than is any *bobbing* display by the Blue Jay.

The emotional gamut, and correlated calls, displays, and postures, exhibited in predator recognition and mobbing seems more restricted than the corresponding behavioral complex of the Blue Jay. Discovery and recognition of a predator by just one Mexican Jay seldom occurs, since the birds seldom travel alone. The stage of "recognition" of the predator comes about sooner after discovery than it does in the Blue Jay, and the general calls of alarm, *reek reek*, are given soon after discovery. Variation in calls thereafter is slight, involving mostly change in intensity of delivery. The reek call may give way in greatest excitement to *ruik ruik*, combination of *ruik* and *reek—ruik-reek*, *ruik-reek* (sounding as if the *ruik* were an inhaled sound, the *reek* an exhaled one).

Mexican Jays exhibit strong displacement behavior when excited by a predator. Jays thus aroused wipe the bill back and forth across the limb on which they are perched when mildly excited (displacement bill-wiping) and either hammer on the perch or scatter leaves or food about with the bill when greatly aroused (displacement foraging). All of these activities are functional in feeding behavior. The birds hammer open hard food-objects, scatter grain or other items of food about in selecting or searching for food, and clean the bill after feeding by wiping it across the perch. The action most

closely associated with feeding (hammering) is the one employed redirectionally in greatest excitement, while that action employed in the time of mild excitement is the least closely associated with feeding of the three redirection activities. It seems that the more completely aroused and frustrated is the bird in the situation at hand, the more completely is it divorced from appropriate motor patterns and transported into patterns functionally typical of another phase of life.

Redirection activity under conditions of stress is frequent and like that of the Blue Jay; a jay in the midst of mobbing a predator chases briefly after a fellow jay.

Reaction toward predators other than birds of prey is similar to that described above. Captive Mexican Jays reacted quickly to a rubber mold of a rattlesnake (*Crotalus sp.*) even though it was a pale yellow in color and resembled a snake only in outline and texture. The birds would not react toward a strip of white paper cut along the same outline as the plastic mold.

Interspecific Relationships of the Scrub Jay

Comments on agonistic behavior of the Scrub Jay will be restricted to discussion of the reaction of the species toward predators. Whereas Blue and Mexican jays react violently toward living and stuffed mounts of predators, my limited observations indicate a different behavior of the Scrub Jay toward the mounted specimens.

In the Sandia Mountains, New Mexico, in the early phase of the nesting cycle, mounts of a Long-eared Owl and a Sharp-shinned Hawk placed near the nest of a pair of Scrub Jays provoked no mobbing reaction. The jays coming to the nest after either mount was installed on a nearby branch flew directly to the nest tree, examined the mount carefully, and then usually went to the nest. On subsequent visits to the nest, the birds would hop to the predator, give the *kwesh kwesh* call of alarm occasionally, but then cease calling and hop onto the head of the specimen and peck in a calm, investigatory manner at its eyes and feathers. After but a brief time the jays would resume their activities, paying no further attention to the mount. When I placed the anterior half of a dead Scrub Jay between the talons of the owl, the birds again examined the mount carefully. Then one of the jays hopped to a branch beneath the owl, reached up and with its bill, extracted the piece of dead jay, carried it off over a nearby ridge of ground, and dropped it.

This behavior would be considered novel under any circumstances in most species of passerines. But in comparing the Scrub

Jay's reaction toward these mounted predators with the reaction at the same time of year (the nesting season) of Mexican Jays and Blue Jays, the behavior is even more puzzling. The strictly territorial behavior of Scrub Jays compared with the irregular territoriality of Blue Jays and the lack of territoriality of Mexican Jays probably accounts for the failure of the Scrub Jays to sound loud assembly calls attracting other jays to the locality of the predator. But the failure of the jays to become at all excited under the circumstances is difficult to explain. The attachment of the birds to the nest site was at this time strong, their behavior was not at all vague but was intense expression of nestbuilding and courtship behavior. The rarity of Sharp-shinned Hawks and Long-eared Owls in the area seems an improbable explanation for relative lack of excitement of the jays, since both species of predator represented by the mounts are also uncommon in the Chiricahua Mountains where Mexican Jays react by intense mobbing display when confronted with the same two specimens. In addition, Great Horned Owls and a Hawk similar to the Sharp-shinned Hawk, the Cooper's Hawk (*Accipiter cooperii*) would seem to offer ample conditioning to the form of the two mounted birds as predators.

Altmann (1956:241-53) studied the reactions of 39 species of birds, including the Scrub Jay, to predators and models of predators. In 19 of these species (not including the Scrub Jay) no mobbing reaction was ever given even under the influence of mobbing reaction of other species. Altmann records encounters of Scrub Jays with owls on three occasions, once with a Short-eared Owl (*Asio flammeus*) model and twice with Screech Owl (*Otus asio*) models. The birds did not mob the first species and mobbed the second species both times, but only secondarily after mobbing of the owls had been instituted by other species. Where Altmann recorded no mobbing of the models (for example, with towhees and thrashers), the birds, in addition, gave no indication that they saw the models; thus, he accumulated little data on failure to respond because of the difficulty in determining whether the models had actually been seen. In the case of the Scrub Jays observed by me, of course, the models were seen.

Hartley (1950:315) in his experiments used mobbing response as the criterion of recognition of a predator. Under this criterion, Scrub Jays did not recognize as predators models of the Long-eared Owl used in the present study and of the Short-eared Owl employed by Altmann. Dr. Richard F. Johnston and Dr. Henry S.

Fitch (personal communication) recall observing Scrub Jays mobbing Great Horned Owls (*Bubo virginianus*) in California (where Altmann's studies were performed). Thus, it seems possible that Scrub Jays give a predator response to Horned Owls because of some conditioning to that species as a predator which conditioning they have not received in experience with the other two species (with which they almost undoubtedly come in contact). Nevertheless the peculiar behavior of the Scrub Jays studied by me indicate that further investigation of the reaction of the species toward predator species is needed.

Social Order in Captive Mexican Jays

A social peck-order existed in the four captive Mexican Jays studied by me. The expression of this form of sociality was best observed in the evening hours, when the birds were preparing to roost, for it was in conflict for and selection of the most favorable roosting sites in the cage that the clearest expression of dominant and subordinate behavior was expressed by the jays. As Tordoff (1954:350) observed in captive Red Crossbills (*Loxia curvirostra*), competition among the jays for roosting sites was severe. Thus, there were more instances of conflict and other interactions, which enabled me to see the social relationships between any two individuals based on many observations in a short time. Increased activity of both Mexican Jays and Red Crossbills at dusk in captivity may be an expression of similar activity in the wild in both species; Tordoff (1954:350) suggested that in the crossbills there is reorganization of the flock after feeding has ceased, in the subsequent flight to roosting areas.

Establishment of Peck-order

Peck-order was not established in these Mexican Jays until several months after they had been placed in the cage. Failure to establish a social order immediately was caused by the slowness of the birds to adapt to captivity, resulting in unnatural behavior at all times. Thus, the birds roosted for awhile wherever they chanced to be when darkness fell. Method appeared in their behavior by approximately the fourth month in captivity, and the adoption of daily routines included the appearance of a peck-order, methodical roosting, feeding, and other behavior.

A rigid peck-order was established by the spring of the birds' first year in captivity. This order was of the straight-line type with no triangles of dominance. This type of order may be characteristic

of the species, but a larger number of birds in the cage might have introduced complexities not expressed with only four birds. The order, although it went through several changes, always consisted of one dominant bird, two middle birds, whose statuses in the order changed twice and were nearly equal, and a low bird, which remained at the bottom of the order throughout this study. The peck-order was maintained by peck-dominance rather than peck-right, interaction between dominant and subordinate individuals always involving aggression on the part of both birds, but always terminating in retreat of the subordinate individual.

Aggression involves jabbing with the bill while the mandibles are being snapped together rapidly, pecking at the carpal region of the wing, at the tarsi, and at the head and bill of a defender. Usually, aggressive interaction is given only when a subordinate bird approaches to within a distance enabling the dominant, without moving its feet, to peck the subordinate. No Mexican Jay ever seeks out his social inferior in order to attack it. Interaction between a dominant and a subordinate bird is practically stereotyped and proceeds as follows (see Fig. 19): The two birds perch side by side, the subordinate standing erect, the dominant bird crouched; either bird may initiate the display. The crouched bird usually lunges at the erect bird, mandibles snapping furiously, and pecks at the tarsi of the subordinate. The erect bird gapes, stands even more erect and then feebly returns the aggression by suddenly crouching and pecking weakly at the tarsi of the dominant. The dominant bird does not move its feet at all, but the subordinate may frequently move about on the perch. No calls are given by either bird. The dominant bird then usually pecks at and grasps feathers in the carpal region of the wing of the subordinate bird. The dominant then pulls at these feathers, and the subordinate draws back, gaping, and fluttering. The subordinate then may again feebly peck at the dominant bird, which in return even more strongly pecks at the tarsi and carpal feathers of the subordinate. If the latter does not then flee, the dominant bird continues pecking at the head, bill, and eventually grabs the bill of the subordinate and pulls until the latter bird flutters free and flees.

The above is a description of a complete interaction between a dominant and a subordinate bird. The activity may be terminated at any time by the fleeing of the subordinate. While such activities usually took place at roosting time they were sometimes instituted in conflict over food or water.

Most interactions took place between the highest and lowest members of the order. The lowest bird seemed habitually to want the roosting place of the highest bird in the order. The choice of roosting place of the dominant bird varied somewhat from week to week, depending probably upon weather conditions. His choice affected the choice of roosting place of all his subordinates. In clear, warm weather, the birds roosted in the open on a horizontal bar, except for the lowest bird in the order, which went to roost last. Although ample space for roosting remained on the bar, the lowest bird always roosted where it happened to be when darkness fell. This was usually in a thicket of branches at the back of the cage. Moreover, while his fellows faced toward the east (presumably toward the direction of the morning sun), the lowest subordinate faced no certain direction—as often as not toward the west. Behavior of the lowest subordinate in roosting was like that of all four birds before they became adjusted to captivity. Thus, perhaps, the basis for the low position of this bird in the peck-order was his failure to adjust to captivity.

Final roosting places were usually fixed by approximately fifteen minutes before darkness, but the activities of competition resulting in the final positions usually began approximately one-half hour before sunset. At this time the birds ceased feeding and began to assume roosting positions for periods of a few seconds to a minute at a time. The dominate bird was always first to display this behavior and selected what to the other jays became the most desired position for roosting. To my eyes this position was hardly different from many other situations in the cage. The position was usually on a horizontal bar held in place by two upright posts and was against one of these uprights. Three other positions existed on the bar next to one of the uprights. Two of these (on either side of the south upright) were never used. The third, on the north side of the north upright post, was often used by the second bird in the order. Thus, the north upright post was all that separated the dominant and his immediate subordinate from each other. The third bird in the order usually roosted on the bar to the north of the second bird. When the birds roosted in the west end of the cage beneath a canopy and on the branches of a limb fastened there, their choice of positions was less consistent.

The dominant bird might have several interactions with the second and third birds in the peck-order in one evening. But long before darkness, the first, second, and third birds in the order had

assumed their eventual roosting positions. Each of these birds took its position again and again, only to leave it to fly about for a few minutes and perch in other places. The lowest bird in the order continued until the end of preroosting activity to fly wildly about, landing near each of the other birds, and when they were absent from their roosting sites, settling momentarily at these places.

The principal difference between the lowest subordinate and the other birds is that the former never took advantage of opportunities to "better" himself in the social order and as regards favorable roosting sites. He occasionally succeeded in pushing one of the others from its roost or in getting situated at one of these places when a bird was temporarily absent from the perch, but if not chased away by any of the higher birds in the order, he deserted the place of his own accord. The three dominant birds seemed always less excited and displayed confidence in their activities as compared to this lowest subordinate. Tordoff (1954:353) noted that in crossbills there were fewer encounters between birds adjacent in the peck-order, except that the despot male was active in dominating the second-ranking bird. In Mexican Jays, the despot interacted most with the lowest-ranking bird, while the birds of second and third rank interacted with no definite preference with each other and with the lowest subordinate.

Occasionally it seemed that the dominant bird of the flock deliberately left its perch and then resumed defense of it against the other three birds, one of which (usually the lowest subordinate) always seized these opportunities to take over this desired roosting place immediately. Table 1 is a summary of interactions between members of the captive group of Mexican Jays, observed on evenings in April, May, June, September, and October.

The lowest subordinate bird of the flock exhibited frustration by a consistent displacement reaction correlated with his inability to gain a roosting place, food, and water. In this reaction, he retired to a perch in a far corner of the cage and hammered with his bill on the perch. When excited by a person, he also engaged in this behavior. The reaction, it will be recalled, is the same as that of wild Mexican Jays when mobbing predators, but never observed by me in other species of jays. The other captive Mexican Jays infrequently indulged in this reaction, which is probably an indication of their greater emotional stability or confidence.

The Peck-order

At the beginning of observations concerning peck-order in my captives, the female RL was probably dominant, since she habitually fed the lowest subordinate, WW, a male. RL's position was taken over within a week after the beginning of courtship feeding, however, by RR, a fully adult male, who thereafter, until his death, was the dominant bird among the captives, feeding WW in courtship, and maintaining dominance at the food tray, water container, and most importantly in interaction concerning roosting sites. From April, 1957, until June, 1957, WL was the second bird in the social order. In roost selection activities, this second position was much inferior to the dominant position and barely superior to the third position. In feeding and drinking activities, the second position was barely inferior to the first position and clearly above the third position. On June 22, RL assumed the roosting position previously occupied by WL, and when the latter came close, RL pecked at him viciously, causing WL to flee.

After RR died in summer, 1957, a prolonged conflict occurred between the second and third subordinates, WL and RL, for the first position among the three remaining birds. This conflict was still taking place on September 26, in the evening of which day WL seemed to dominate RL and finally assumed the roosting place for which they had competed. WW continued to fly about and was pecked several times by both RL and WL. Thus, WW remained the lowest bird in the order. To my knowledge, the

TABLE I.—A Record of Observed Conflicts of Peck-dominance in Captive Mexican Jays Based on 65 Encounters

Aggressive dominance in an encounter	Subordinance in an encounter					Percent of conflicts in which bird was dominant
	RR	RL	WL	WW	Total instances of dominance	
RR	.....	5	5	39	49	98
RL	1	.....	2	7	10	53
WL	0	4	.....	2	6	46
WW	0	0	0	.....	0	00
Total instances of subordinance	1	9	7	48	65 (total encounters)	

social order of these birds did not change again during the life of the captives.

I have previously discussed (p. 34) under the significance of courtship feeding and its relationship to social order, the possible reasons causing feeding of a male by a female in captive Mexican Jays and its meaning in social order among these jays.

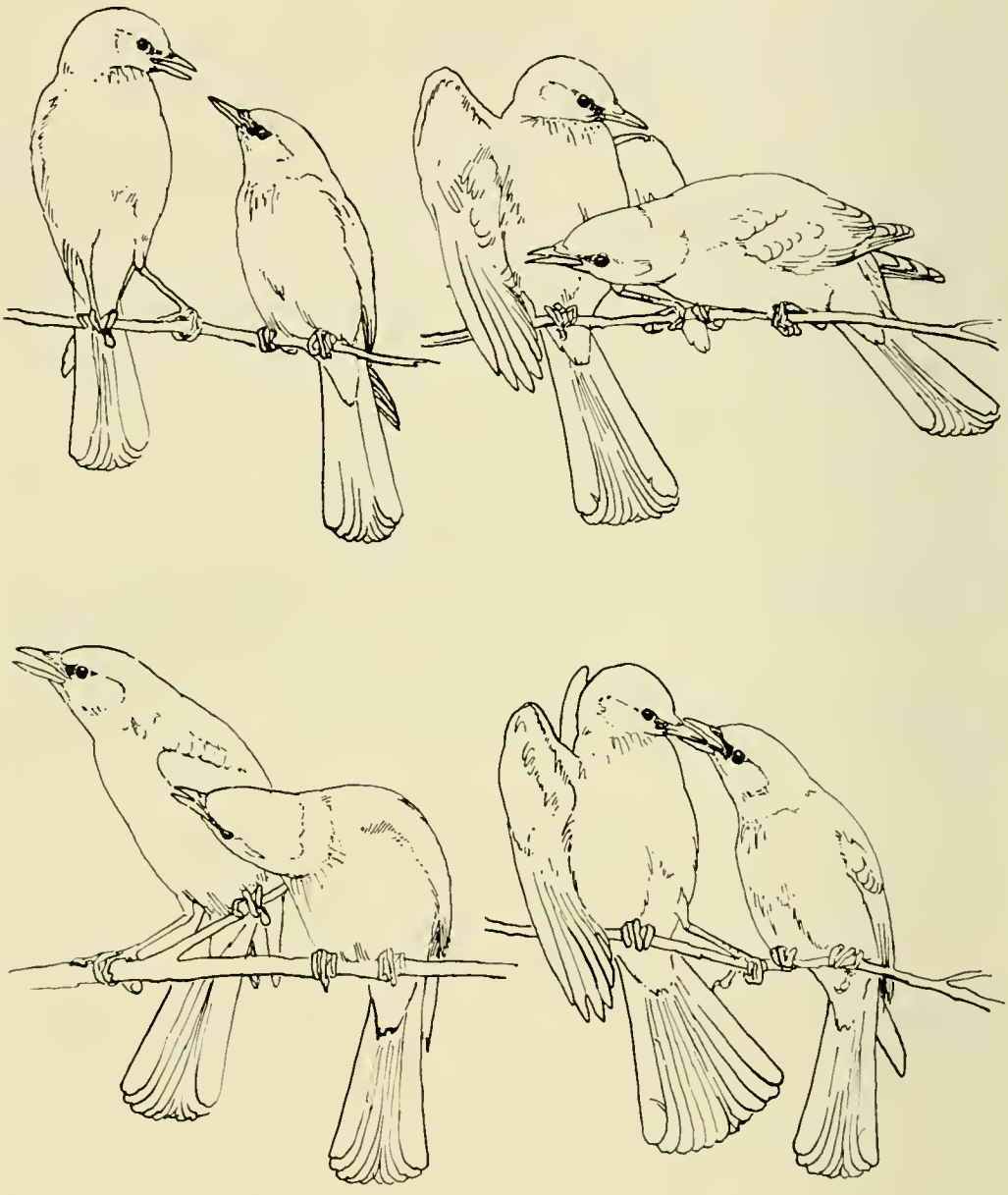


FIG. 19.—Illustration of phases of conflict between dominant (bird on right in each pair) and subordinate (left). Upper left, subordinate flies to perch beside dominant preparing to roost and assumes erect posture. Upper right, dominant first pecks at tarsi of subordinate, which attempts to back away but then may feebly return peck at dominant. Lower left, dominant then seizes carpal feathers and pulls, causing subordinate to flutter or pull away. Subordinate then may again peck feebly at tarsi of dominant or may flee. Lower right, dominant grasps bill of subordinate and pulls strongly, causing subordinate to pull away and (usually) flee.

Miscellaneous Behavior

Investigatory Behavior in the Blue Jay

Investigatory behavior in the Blue Jay is displayed toward strange animals, new food supplies, or other objects arousing curiosity on the part of a jay. This behavior is perhaps most often expressed in the investigation of food-objects in the course of foraging behavior. A jay will fly directly toward a newly-discovered food supply, veer suddenly, and alight a few feet away from it. The bird then assumes the posture of investigation (Fig. 4). The head is moved from side to side as the bird eyes the food first with one eye, then with the other. The jay then hops around the sides of the area containing the food and gradually works its way closer. Any unnatural movement by the object or near it will cause the jay to jump quickly into the air and land several feet further away from the food. The bird will take food eventually if not alarmed, but at first will take small particles quickly and not eat them at the source of supply. Gradually, as the bird gains confidence, it may come to eat at the source of supply instead of first flying to a nearby perch. But the investigatory behavior may be resumed and the air of caution again displayed at the first hint of unnatural circumstances. This cautious attitude is characteristic of the Blue Jay in most of its "vegetative activities." It contrasts in part with the attitude of the Mexican Jay under similar circumstances.

Investigatory Behavior in the Mexican Jay

Mexican Jays are less wary than Blue Jays in approaching a strange object. Food placed in an obvious place attracts only one or two cautious Blue Jays, which come to the supply slowly and carefully. But in contrast a flock of from five to ten Mexican Jays may swarm over a like food supply within minutes after its discovery, all the birds beginning to feed or carry off the food after only a brief examination. The posture of investigation (erect, hopping stiff-legged) of the Mexican Jay is similar to that of the Blue Jay but less exaggerated. Doubtless, the degree of exaggeration of this posture is a function of the degree of wariness. No attempt is made by any individual Mexican Jay to monopolize the food; each bird selects bits of it, eats on the spot, or carries it a short distance to a perch. In the latter case, however, the food seems not to be taken quickly away in an expression of fear of the place where the food source is located. The comparative lack of caution displayed by this

species in comparison to the Blue Jay is possibly a function of greater sociality.

The few times that I have observed Scrub Jays reacting to strange objects, they also displayed little development of investigatory behavior and approached a food supply especially provided precisely as did the Mexican Jays, although not in a flock. (It will be recalled that these same Scrub Jays reacted to a stuffed Long-eared Owl with little of the caution displayed by Blue Jays in the investigatory behavior.)

Anting in the Blue Jay

Anting is commonly indulged in by Blue Jays according to Whitaker (1957:251) in her thorough analysis and complete bibliography of records of anting.

Blue Jays actively perform anting; that is, they pick up ants in their bills and apply them to their plumage, instead of letting them crawl up their legs. Davis (1950:518-9) observed a jay perched in an oak tree, picking ants off the leaves and placing them deeply beneath the contour feathers of the body. According to Laskey (1958:214) anting Blue Jays she observed rested on their tails while applying ants to the primaries; afterward one jay rubbed a dry leaf along the primaries. Ivor (1943:52) believes that ants are always applied to the ventral surface of the outer primaries, from just below the wrist to the tip of the wing. According to Whitaker (1957:249) a pet Orchard Oriole applied ants to several parts of the posterior half of the body, bases of the rectrices, and wings.

I have received from Dr. Edwin C. Galbraith an account of an adult Blue Jay that anted in Galbraith's backyard almost daily for over a week. The bird came to the yard and stood on a small anthill, picked up the ants, and applied them to its plumage.

When my two young captive Blue Jays were approximately 40 days of age, I released a host of ants (*Pogonomyrmex sp.*) on the floor of their cage. The birds at once became so frightened, flying headlong around in their cage, that I feared that they would injure themselves. The ants utilized here were, of course, of an unacceptable species, one that possesses a functional sting (Whitaker, 1957:206).

When the young Blue Jays were approximately 57 days of age, I placed a shallow tray containing about 20 ants of the genus *Dorymyrmex* into their cage. Ants of this genus have been found acceptable for anting purposes (Whitaker, 1957:202), probably because they do not sting and are odoriferous. The species of ant

utilized in the present experiment was bright lemon yellow in color and was taken from beneath stones on the grounds of the Southwestern Research Station in southeastern Arizona.

A Blue Jay exhibited interest and no fear when the *Dorymyrmex* were presented. Hopping near the ants crawling on the floor of the cage, the bird maintained a stiff-legged investigatory posture. With neck outstretched and crest erect, he peered at the ants and at the same time uttered a strained weak conversational note. After several false starts, the bird jabbed hard with his bill and secured an ant. The bird sometimes actually ate several ants before anting, being first stimulated to ant when one of the insects escaped from the bill and crawled over the face of the bird. Then in quick succession the jay usually took several ants and tucked them swiftly under the primaries halfway to the tip of a wing.

Anting in the Mexican Jay

I was not able to induce Mexican Jays to ant in captivity. There are no published records of the species anting, though anting of some type is found generally throughout the family Corvidae (Whitaker, 1957:234-5). Release of ants (*Dorymyrmex sp.*) into a cage containing two juvenal Mexican Jays elicited no response from the birds, although juvenal Blue Jays anted with the same kind of ant. In one experiment, several hundred individuals of a harmless, odoriferous species of ant (species not as yet determined) were placed in a shallow tray, the edges of which were coated with petroleum jelly to retain them. The tray was then placed on a prominent limb in the flight cage containing the four Mexican Jays. The birds immediately showed interest in the ants but did not ant. Instead, they ate all but the few of the insects that escaped and then set about devouring the petroleum jelly! It seems possible that Mexican Jays do not ant on the basis of this experiment and lack of positive evidence to the contrary in the literature.

Goodwin (1953:149) concludes that the type of anting behavior is probably adaptive to different ecological situations and is not correlated with phylogeny. Therefore, possibly, the failure of a species to ant cannot be utilized as a valid character in plotting systematic relationships. Of course, the lack of correlation of *method* of anting and phylogeny may not be the same sort of problem as is involved in comparing two species of birds, one of which ants and one of which does not ant. In the latter problem, anting may have phylogenetic implications.

Tail-wagging: Preroosting Behavior in the Mexican Jay

Preroosting social behavior of Mexican Jays in captivity has been discussed in the previous section concerning social behavior. A certain behavioral trait that I have termed tail-wagging is not connected with sociality in Mexican Jays but is an integral part of preroosting behavior. In tail-wagging, each of my captive Mexican Jays upon settling in its chosen roosting site drew in its neck, fluffed its feathers, rested low on the perch, and then gently wagged its tail quickly from side to side, three to six times. If the bird then proceeded to sleep, it did not wag its tail again, but if it chose to rearrange itself in any way before sleeping, it again performed the tail-wagging activity. None of the other jays that I kept in captivity exhibited this behavior, including the young Mexican Jays. I have not observed jays in the wild going to roost.

Tail-wagging may be a subtle method of plumage arrangement connected with "getting comfortable" for roosting, or an expression of "contentment" or "satisfaction" connected with the termination of activity and the coming to rest for the night. I have found no references in the literature to similar behavior in other birds. Tail-flicking and wing-flicking, which are considered by Andrews (1957) to be intention movements of flight, would not seem to be homologous to tail-wagging, since certainly the most remotely possible intention of tail-wagging is flight. The fact that I have failed to observe the behavior in other jays might be of significance in systematic considerations.

PART III—PHYLOGENY AND SYSTEMATICS

SOME ASPECTS OF THE PHYLOGENY AND SYSTEMATICS OF NEW WORLD JAYS

The preceding discussion of the behavior of jays has led to a consideration of phylogeny and systematics of New World jays. The following account is based also on behavioral investigations of other workers and information on morphology and distribution.

Existing Classifications

New World jays exhibit a marked diversity in morphology, behavior, geographic and ecologic distribution. Early classifications (*cf.* Ridgway, 1904; Sharpe, 1909; Hellmayr, 1934) necessarily were based on the superficial aspects of these four factors; a large number of genera and species were proposed for the western hemisphere. Current views on classification of these birds are but

slight modifications of those of the earlier authors. Detailed study of the osteology and myology of jays provides a picture of their systematics wholly different from that established by the above criteria. Studies by Ashley (1941) and Hudson (1955) emphasize the muscular and skeletal uniformity within the Corvidae. A classification of jays based on these two systems of the body would greatly reduce the number of genera and species.

The most recent classification of the Corvidae is that of Amadon (1944a); this attempts to offer a compromise between the disparate views outlined above. Amadon seemingly bases his views on conservative morphology and behavioral characteristics, although this is not always evident in his discussion. Often his alterations seem negatively conceived; that is, there is a tendency to minimize the importance of external morphology but a concomitant failure to provide other, positive bases for his proposed arrangement. There also seems to be a primary interest in "lumping" in order to arrive at a classification containing an average of five species per genus (*cf.* Mayr, 1943:138-9), rather than an interest in attaining a natural organization of genera and species.

I believe that ornithologists will not accept Amadon's alterations without more positive evidence in favor of them. Nevertheless, Amadon's classification is more realistic than its predecessors; there is in it the concept of the New Systematics, in which, for example, the genus is regarded as a category indicating relationship between its members.

The genera *Cyanocitta* and *Aphelocoma* are widely distributed in North America. These genera have been united with *Cissilopha* and *Cyanolyca* of Mexico, central, and South America, as a single genus, *Cyanocitta,* by Amadon (1944a). *Calocitta* (Magpie-Jays of Mexico and central America), *Psilorhinus* (Brown Jays of Mexico and central America), and *Cyanocorax* (Green Jay and "Tufted" Jays of North and South America) are considered to be distinct genera in all published works of modern status.

The genus *Cyanocitta* (in the restricted sense) consists of two species, *C. cristata* inhabiting deciduous forests of western North America south to central America. The genus *Aphelocoma* comprises three species, *A. coerulescens, ultramarina,* and *unicolor. A. coerulescens* inhabits western North America from Washington and Wyoming south to southern Mexico and, disjunctly, peninsular Florida. *A. ultramarina* inhabits western North America from the

southwestern United States to Southern Mexico. *A. unicolor* inhabits tropical forests of southern Mexico and central America.

Pitelka (1951) presented an excellent account of geographic distribution and subspeciation, based primarily on morphology, in *Aphelocoma.* No similar task has been undertaken for *Cyanocitta.* The two genera show striking dissimilarities; for example, there are crests and barred feathers in wings and tail in *Cyanocitta,* not in *Aphelocoma.* Amadon (1944a) and Pitelka (1945, 1951) have, however, shown that many characteristics formerly believed to be confined to a certain taxon of jays, or thought to be invariable within a taxon, are not at all thus. A reevaluation is in order: some characteristics need to be discarded or reduced to their proper status; many others, some heretofore not well known and some documented in the literature but ignored or overlooked, need to be included.

Corvids as a group have a sum of distinctive behavioral and morphological characteristics that make them a well-defined family. Amadon (1944a:2) has enumerated these characteristics, which will not be listed here; they show little or no variation from one species to another and thus are not of use in considerations of phylogeny *within* the Corvidae. Following is a discussion of behavioral and morphological variation of and within the previously mentioned seven genera of New World jays thought to be of New World origin, including an attempt to elucidate several aspects of the systematic and phylogenetic relationships of these groups.

New Considerations

Since behavorial studies in only *Cyanocitta, Aphelocoma,* and *Calocitta* were formally undertaken by me, and since data in the literature on the seven genera are uneven at best, it would be presumptuous of me to attempt any readjustment of the classification of New World jays. However, it is my opinion, based on the behavioral and morphological characteristics possessed by each of the groups *Cyanocitta* and *Aphelocoma,* considered in greatest detail in this paper, that they should be regarded as distinct from each other. Evidence concerning this belief as well as concerning the other genera under consideration causes me to believe that there are two main evolutionary "lines" of New World jays, on a combined behavioral-morphological basis.

These two evolutionary lines are here termed, for the sake of brevity, the "Inornate line" and the "Ornate line." The fact that there is ornation of a sort in some forms of the first line and lack

of ornation in some forms of the second line is an indication that these terms alone do not describe the respective postulated lines but only comparatively characterize them as a whole.

The "Inornate line" includes, definitely, only the members of the genus *Aphelocoma*. The characteristics of this line are, for the most part, more conveniently expressed negatively in the course of enumeration of certain "positive" characteristics of the "Ornate line." The latter as here conceived contains five of the remaining six genera to be considered here, *Cyanolyca* being omitted from inclusion in either line because I consider that behavorially the genus is so little known that its documented characteristics cannot be (logically) assessed at this time.

One other genus, *Gymnorhinus*, will be omitted entirely from the following discussion. The evidence that it is of New World origin is entirely inconclusive. Amadon's (1944a:7-8) discussion of evidence for and against inclusion of the Pinyon Jay in the assemblage of jays of New or Old World origin is interesting, but his opinion, ". . . that a perponderance of evidence indicates relationship of *Gymnorhinus* to *Cyanocitta* . . ." is not justifiable on the basis of the far from conclusive data that he presents. One behavioral trait alone, the fact that the Pinyon Jay walks and runs instead of hops (see for example Bent, 1946:307) would seem to call for a postponement of its "final" placement systematically. So far as I know, all other jays in the New World hop exclusively, and this walking and running in *Gymnorhinus* implies a rather different neuromuscular system, one perhaps more like that of the Corvinae, whose members also walk and run and are unquestionably of Old World origin.

The "Ornate line" is characterized as follows, with characteristics of the "Inornate line" contained in parentheses:

1. Tendency for the development of crests (no crests).
2. Tendency toward specific complexities of plumage pattern.
   A. Dark colored bib on upper chest, varying from pale to distinct but always solid (streaked or otherwise discontinuous bib, whether pale or distinct).
   B. Prevalence of pale-tipped-whitish or yellowish-rectrices (always uniform bluish above, gray below).
   C. Discreet head markings such as bridles, malar patches, etc. [Fig. 24].
3. Tendency, at least in most ornate genera, for presence of two vocalizations—the "pump-handle" call and the "squeaky-gate" call (no such calls), as well as for the assembly and/or alarm calls to be downwardly inflected or uninflected (upwardly inflected) in all genera of the line.

The above characteristics merely serve to distinguish the two proposed evolutionary lines but by themselves do not help to elucidate the intricacies of evolution and relationships in or between the two groups. For this reason their discussion is reserved until later in this paper.

It is, I think, in the matter of trends in degree of sociality and relatively direct morphological correlates of these trends that some indication of the phylogeny of New World jays may be most accurately perceived. The postulated patterns of these trends are better illustrated in the "Inornate line" of jays and then applied to the discussion of the "Ornate line," after which the aforementioned characteristics distinguishing the two lines may be related to the social trends. Finally, a comparison of certain little known characteristics between and in certain genera is appropriate; these characteristics do not at this time seem to be related to the concept of phylogeny of the jays as a whole and are mentioned merely for future reference.

Sociality and Phylogeny in *Aphelocoma*

I have previously given evidence of the highly social, semicommunal habits of the Mexican Jay in Arizona. The lack of territoriality of pairs in this subspecies, *A. u. arizonae*, contrasts with habits of some of the other forms of jays under consideration in this paper. The Scrub Jay, throughout much of its range, has, as described, strongly-developed territorial habits, and has long been considered a congener of the Mexican Jay. What is the temporal sequence of evolution of these two phenomena in *Aphelocoma*, and what bearing does information concerning the degree of sociality possibly have upon phylogenetic considerations in the genus and in other New World jays?

In the following discussion of sociality and its correlation with phylogeny, I shall employ the term territoriality without qualification to indicate a social condition in the breeding season in which the breeding population consists of male-female pairs, each of which inhabits a given area within the habitat. Each pair, moreover, defends this area or territory against other breeding birds of the same species and reveals at least in a general way the boundaries of its territory in any direction from the nest site by territorial behavior (singing, fighting, making self conspicuous) between the nest site and point on the boundary and lack of this kind of behavior beyond such a point. Because there are, I believe, degrees of territoriality, its most extreme form in jays as just de-

fined will occasionally be termed territoriality of pairs. The Blue Jay is territorial or social in the breeding season in the manner just defined. Intermediate conditions of sociality in the breeding season occur in which pairs are formed and carry out nesting in a given area without, however, revealing much in the way of territorial behavior or with occasional helpers at the nest. The Florida Scrub Jay may as we shall see tentatively be placed in this category along with the Magpie-Jay. Finally, at the opposite extreme in New World jays, is a social condition in the breeding season characterized by semi-communal nesting, nonbreeding helpers at the nest, and maintenance of flock structure throughout the nesting season. The Mexican Jay in Arizona and the Brown Jay (*Psilorhinus*) are species exhibiting such breeding sociality. It is true as I have previously stated that at least in the Arizona Mexican Jay each social breeding flock may inhabit a given area, perhaps excluding from it other such flocks, thus maintaining a kind of territory. But for purposes of the following discussion this sense of the term territoriality will be ignored.

There is probably nothing inherent in either territoriality or more social habits that make either mode of existence more primitive than the other. Both phenomena probably were found in reptilian ancestors of birds, and doubtless both have appeared and disappeared independently many times in birds. It is not possible to state which type of sociality is the most primitive in *Aphelocoma* or New World jays as a whole. We will herein speculate on the resolution of this problem, using the limited evidence available.

The Case for the Primitiveness of Territoriality

Indications from analogy.—In other groups of birds in which territoriality of pairs and a high degree of sociality are known in different species, there is evidence that the former condition is primitive and a high degree of sociality represents a condition of more recent origin. By analogy, the primitiveness of territoriality gains favor in speculation.

Davis (1942) presents an excellent account of the probable course of evolution of communal nesting in the Crotophaginae—the anis, family Cuculidae. In addition he reviews the literature on the subject, pointing out the analagous origin of highly social habits, in the breeding season at least, in many unrelated families of birds such as Picidae (*Melanerpes*: Ritter, 1938), Fringillidae (*Philetarius*: Friedmann, 1930), and Timaliidae (*Yukina bruneiceps*: Yamashima, 1938).

For the Crotophaginae, Davis (1942) describes the decreasing degree of territoriality of pairs from the weakly territorial *Guira* through *Crotophage major* to *C. ani* and *C. sulcirostris*, the last two of which are communal nesters with several females laying eggs in the same nest. Davis shows that *Guira* is morphologically closer than *Crotophaga* to other possibly related Cuculids that are territorial. He also points out physiological characteristics (spontaneous ovulation), vocal characteristics (a strong flock call, greater variety of calls, and no song), and morphological characteristics (small, degenerate crest) that he relates to communal habits, decreased sexual fighting, and general lack of courtship.

Davis believes that the course of evolution to social nesting in anis involved three primary factors: (*a*) modification of territorialism; (*b*) abberrant breeding; (*c*) type of habitat. In the changes from *Guira* to *Crotophaga ani*, territory of pairs is reduced and territorial defense by a group is greater, accompanied by increase in polygamy. Davis suggests that there is a "proclivity" in Cuculidae for the development of aberrant breeding habits, citing social parasitism in the European cuckoos. In the anis he believes that this proclivity, under the influence of environmental restrictions (type of habitat for breeding and roosting seeming to be restricted to islands of trees in savanna) provides selection pressure for the evolution of a high degree of sociality.

Indications within Aphelocoma.—If territoriality or other low degree of sociality is primitive in *Aphelocoma*, we may properly assume that the immediate ancestral form of the genus was a territorial species. Is there a living group of Neotropical jays, exhibiting low sociality and showing a basic morphological resemblance to *Aphelocoma*? *Cyanolyca* is seemingly the only genus even vaguely fitting this description. Although it cannot be logically placed in either evolutionary line previously postulated, two species, *C. pumilo* and *C. nana* bear proportional similarities to *Aphelocoma*, *C. nana* exhibits some resemblance in plumage pattern to the "Inornate line," and at least some of the species are not highly social in the breeding season (*cf.* Dickey and Van Rossem, 1938:410-11, concerning *C. pumilo* for an example). Because of these indications, *Cyanolyca* may be ancestral to or have a close relationship by immediate ancestry with *Aphelocoma*.

Assuming that the Mexican and Unicolored jays (*A. ultramarina* and *unicolor*) arose from ancestral *Aphelocoma* stock or from *A.*

coerulescens itself, what are the evidences that degeneration of morphological and behavioral characteristics possibly important in courtship and sexual fighting in the territorial ancestor have occurred with the acquisition of more social habits? Both the Mexican and Unicolored Jays exhibit a color pattern basically like that of the distinctly-patterned Scrub Jay, but much less distinct. There is age dimorphism in bill coloration—possibly significant in recognition of sexual development or individual identity in flocks of closely integrated birds. In *A. ultramarina,* at least, there is a strong assembly (flock) call, although the variety of calls in the repertoire is less than in the territorial Scrub Jay. There is in the Mexican Jay in Arizona, at least, little if any sexual fighting, little courtship feeding in the wild, and a strong development of ritualized behavior concerned with social hierarchy.

The development of a degree of sociality in the Scrub Jay in Florida greater than in other, territorial, races in the West may be of much more recent appearance than, and only analogous to, the condition in the Mexican Jay. In the Floridan race the plumage pattern is distinct as it is in related territorial subspecies, and there is no external indication of age dimorphism in bill color of adult birds. There is a wide geographical separation of the race in Florida from the other species of the genus with non-territorial habits.

Sociality in the family Corvidae.—There does not seem to me to be a trend in sociality within the Corvidae. Highly social and territorial habits as well as degrees of sociality intermediate to these occur in genera throughout the range of the family.

Discussion.—On the basis of the preceding discussion a fairly logical case can be constructed for the primitiveness of territoriality in *Aphelocoma* at least, although not for New World jays as a group or corvids as a whole. From analogy there is precedent for territoriality giving rise to more highly social habits. However, in the following section dealing with the opposite view, a closer examination of the social habits and possibly correlated morphology of *Aphelocoma* as well as the other New World jays reveals evidence for the view that the evolutionary trend has been from a high to a low degree of sociality. Moreover, with a certain amount of success these indications of trends in sociality can with logic be applied to the problem of mapping the phylogeny of New World jays.

The Case for the Primitiveness of More Social Habits

Behavioral and distributional evidence within Aphelocoma.—If a gregarious type of existence is the most primitive form of sociality of the breeding season in *Aphelocoma,* we may assume properly that the immediate ancestral form of the genus was atterritorial and gregarious.

In the race of the Scrub Jay, *A. c. coerulescens,* in peninsular Florida, the phenomenon of helpers at the nest has been definitely established by Grimes (1940:433), and judging from the literature, territoriality is not prevalent in the race. This Florida race is, however, by no means as social as the Mexican Jay in Arizona, since Amadon (1944b) studied the nesting habits and did not observe helpers at the nest. The form in Florida is unique in that it is well isolated geographically from other races of the species. Since the individuals of the species are relatively sedentary, it seems probable that the colonization reaching Florida occurred northward into the southwestern United States and thence along the Gulf of Mexico to the peninsula. This colonization probably took place early in the history of the Scrub Jay's evolution. Seemingly, nothing is known about the social breeding habits of the races of the Scrub Jay in southern Mexico (*A. c. sumichrasti* and *remota*). Since the race in Florida is so much more social than, say, *A. c. woodhouseii* of the western United States, it is tempting to believe that *A. c. coerulescens* is not only a relict, isolated in the early stages of evolution of the species, but that its tendency to possess more social breeding habits than those known for other races is also relict, representing the primitive condition in the species, from which the territorial forms have sprung. Moreover, it is practically certain that knowledge of the sociality of the poorly known races of the Scrub Jay in Mexico will shed additional light on this problem.

Correlation of sociality and age dimorphism of bill color.—Although much behavior data, mentioned above, are still to be gathered, or at least made known, there are morphological data available to support the speculation that highly social habits are primitive and less social habits derived from this condition in *Aphelocoma* as well as in other New World jays.

In *Aphelocoma ultramarina* (except *couchii* and part of *sordida*), *A. unicolor, Psilorhinus,* and *Cissilopha,* there is prolonged age dimorphism in bill color, the young having parti-colored bills for periods varying from one year to several years, as is discussed else-

where in this paper. Highly social nesting habits exist in *Aphelocoma ultramarina arizonae, Psilorhinus* (Skutch, 1935:261-5), and probably in *Cissilopha* and *Aphelocoma unicolor.* Concerning *Cissilopha,* my own observations of *C. beecheii* indicate strong flocking tendencies much like those of *Psilorhinus.* Since Amadon (1944a:7) and Sutton (1951:233) have both indicated the close similarity of the four species in *Cissilopha* (suggesting they be considered as one superspecies and as subspecies of one species, respectively), there is good reason to believe that degree of sociality in the species *C. beecheii* is representative of the entire genus. As for *A. unicolor,* Dickey and Van Rossem (1938:409) collected all five members of a flock in cloud forest in El Salvador; of these specimens, four were males in breeding condition and one a female that would not have laid eggs for some weeks. The fact that all five of the flock's members were collected indicates a high degree of sociality in the species, comparable to that in *A. ultramarina arizonae;* in less social species where the individuals exhibit little "loyalty" to each other, one shot will characteristically result in one specimen killed and quick dispersal of the remaining birds in several directions. Also the presence of four males in breeding condition associating in the same flock indicates a highly social nature. Pitelka's (1951:358) observations of *A. unicolor* also strongly indicate highly social breeding habits similar to those in *A. u. arizonae.* He found groups of up to nine individuals (each containing both adults and first year birds) settled in restricted areas. A nest with eggs was found in each of two of these areas, while in a third area a group of jays were attending at least two fledglings.

In *Aphelocoma coerulescens, Cyanolyca, Calocitta, Cyanocorax* (except the "Coronideus group," if *C. violaceus* is typical), and *Cyanocitta,* no externally visible evidence of parti-coloredness exists on the bill, at least after postjuvenal molt is underway; such a condition hereafter will be referred to as lack of age dimorphism in bill color, even though juveniles of these forms have parti-colored bills. In these jays there is a comparative lack of sociality, and territoriality of pairs in *Cyanocitta* and *A. coerulescens* of at least races *woodhouseii, oocleptica,* and *californica.* The race *woodhouseii* is of Pitelka's 1951 "Woodhouseii group," while races *oocleptica* and *californica* are contained in his "Californica group," which may be reason for believing that all races of these two groups are socially similar, since their ranges are either continuous, are at most separated by narrow geographic gaps. Dr. Pitelka

does, however, emphasize to me in a letter that ecological differences, and differences in population density among the races of these two groups and especially between sparsely distributed inland populations, such as compose *woodhouseii,* and coastal populations, as in central California races, may have direct bearing on degree of sociality. Consequently, coastal Scrub Jays appear more social that what I have referred to as highly territorial Scrub Jays in New Mexico. In addition Pitelka refers me to the fact that in California, flocks of first year Scrub Jays may persist well into spring. This last characteristic is also found in the Blue Jay, as I have previously mentioned. The latter is territorial in pairs, revealing no social phenomenon such as helpers at the nest.

Helpers at the nest and similar habits involving co-operation of more than two birds in the care of nest, eggs, and young, have proved to be fairly easy to detect when characteristic of the species under observation. It would certainly be surprising to me if at this late date such habits were found to exist in the California races of the Scrub Jay. In addition, Amadon (1944b) was unable to detect in the Florida Scrub Jay defense of territory or existence of specific or general boundaries recognized by pairs of Scrub Jays inhabiting adjacent areas, while such evidences of territoriality of pairs are known in Scrub Jays of the western United States, inland and coastal populations alike. Thus, I submit that while coastal Scrub Jays may be more social in the nesting season than inland western forms of the species, both the "Woodhouseii group" and the "Californica group" are characterized by less social breeding habits than *A. c. coerulescens* of Florida.

There is evidence of helpers at the nest in *Calocitta* (Skutch, 1953:69), and my own experience with Magpie-Jays in Sonora, indicate that in the nesting season at least there is frequently definite separation into pairs.

Dickey and Van Rossem describe pairing and nesting in *Calocitta* without mention of the assistance or presence around the nest of other individuals. Edwards and Lea (1955:47) speak of the birds being in pairs in spring.

Cyanocorax also seems to be a group in which the degree of sociality is less than in *Psilorhinus* but in which flocking is common and strict territoriality of pairs is not well-developed. Thus, although Moore (1938:238-9) speaks of pairs of Tufted Jays (*Cyancorax dickeyi*), he also mentions the appearance of third individuals at the nest on occasion, adding that if this represented helpers at

the nest, he and companions "did not see the complete picture." I have not found any evidence in the literature of highly social habits in the nesting of the Green Jay (*Cyanocorax yncas*), although these birds often flock conspicuously outside the nesting season. Sennett (1877:29-30) states that in April, Green Jays were in pairs at Hidalgo, Texas, and also mentions pairs at nests. On one occasion Sennett shot one member of such a pair, and another time he collected both members of a pair. Prominent age dimorphism in bill color is thus characteristic of some highly social species or species thought to be so, but is absent in less social and territorial species. Is this correlation of any significance or due to chance?

Possible social adaptiveness of age dimorphism in bill color.— It is probable that individual Mexican Jays with parti-colored bills do not themselves breed but only assist older breeding birds in reproductive duties. Thus, in a flock of Mexican Jays at one nest, it is possible that different bill patterns correlated with different statuses in the flocks—different duties, different degrees of sexual maturation—might serve as signals of these statuses and thus facilitate social interaction in such closely integrated groups. Although this dimorphism might be nonadaptive and be explained merely as due to genic pleiotropy of correlated responses, in this situation pleiotropy or correlation and adaptiveness may be associated logically. Thus, it may be that since parti-coloredness disappears as maturity is reached, the phenomena of rate of maturation and duration and extent of parti-coloredness are two expressions of a single gene or set of genes.

Having postulated a logical if unproven adaptive value of prominent age dimorphism in bill color in the most social jays, what is the possible significance of lack of such a signal characteristic of immaturity in territorial jays? While there are no records of individuals with parti-colored bills in the Mexican Jay actually breeding, there are records of breeding of first-year individuals of the Blue Jay, as stated previously. Blue Jays are territorial, never in their first nesting season assist older birds, and actually nest themselves; it may logically be assumed that first-year Blue Jays are capable of breeding before their counterparts in the Mexican Jay. There is, as a result of this rapidity of Blue Jays to mature sexually, no adaptive value in Blue Jays for, let us say, a four-year-old adult distinguishing on any morphological basis between another four-year-old potential mate and one that is one year old, particularly if the latter is present on the breeding grounds during pair formation

and actively participates in courtship. The same is probably true in other, territorial, or at least not highly social, jays.

Evolutionary significance of bill color and sociality.—Now, if the less social condition in jays is accompanied by age dimorphism in bill color, it would be expected that forms becoming progressively less social would be maturing more rapidly, and that the duration of parti-colored bills associated with immaturity would gradually be shortened. If age dimorphism in bill color is controlled by the same gene(s) that effects the rate of maturation, it explains the disappearance of parti-coloredness to state that the other expression of its causative gene(s) is being selected against. However, even if the dimorphism is under separate control the condition of becoming sexually mature early and yet because of pied-bill being relegated to subbreeding status would cause that part of the population possessing the combination of these generally opposed characteristics to be gradually selected against.

There is morphological evidence in the ontogeny of individuals of less social and territorial jays such as *Aphelocoma coerulescens woodhouseii, Cyanocitta, Calocitta,* and *Cyanocorax yncas* that this elimination of parti-coloredness did in fact occur in phylogeny. In these forms, a distinctly pied condition is maintained on the *inside* horny surfaces of the mandibles long after the outside of the bill has become indistinguishable in color from that of the adults of the species (*cf.* Nichols, 1955:27 for discovery of this characteristic in the Blue Jay). The inside surface of the bill is exactly the place where this parti-coloredness could be expected to persist—a place where it is not selected against, may disappear haphazardly and slowly, reflecting an ancestry in birds with parti-colored bills. In all of the forms under discussion that are black-billed as adults, a stage of exterior parti-coloredness is passed through but is completed sometime around or before the postjuvenal molt. Figure 21 shows a young Steller's Jay just out of the nest and in juvenal plumage. Note that its bill closely resembles in color that of the Mexican Jay at least a year old in Figure 20. Figure 22 shows the same Steller's Jay in the early stages of postjuvenal molt. Note that the bill is now practically indistinguishable from that of a black-billed adult, although the yellow integument of the gape is still evident.

The rate of disappearance of the parti-coloredness inside the bill is variable with the species. In *Cyanocitta* and *Aphelocoma c. woodhouseii* all trace of the condition is lost by sometime in winter

of the first year. However, in *Calocitta*, which is more social than the species of *Cyanocitta*, for example, the parti-coloredness inside the bill persists in some cases for over a year.

There is the possibility in these species possessing parti-coloredness only inside the mouth after juvenal life, that the condition is an adaptive one, not a relict, and functional—possibly even the "beginning" stage in the evolution of more prolonged and extensive parti-coloredness of the bill in species that are becoming more social. This can be discounted for the following reasons. The characteristic could hardly be adaptive as a signal facilitating the recognition of the bearer's social status or maturity since as pointed out parti-coloredness does not persist until the following breeding season in some species and is hardly conspicuous enough in year-old Magpie-Jays to serve such a function. It cannot be assumed that adults of *Cyanocitta* or *Aphelocoma coerulescens woodhouseii* respond to the parti-colored internal surfaces of the bills of gaping young birds; adults probably respond instead to the gaping action itself, since the response of the adult male to the begging, gaping female in courtship is exactly the same, and she does not have this color pattern inside the mouth.

Intra- and interspecific variability in duration of parti-coloredness.—External parti-coloredness in bill color disappears in young of *A. ultramarina couchii*, and populations of *A. u. sordida* exclusive of southern Hidalgo, Mexico, (hereinafter referred to as *A. u. "sordida*—1" as opposed to the remainder of the subspecies "*sordida*—2"). In these birds "the bill darkens rapidly during nestling life and becomes black before or during postjuvenal molt (Pitelka, 1945: 257)", in a manner similar to that in *Cyanocitta*. As in the latter genus, parti-coloredness remains inside the bill for some time after it disappears externally.

Although I have little field experience with *A. u. couchii*, other workers have noted its habits in enough detail that they may be compared to those of *A. u. arizonae*. If age dimorphism in the bill in this species is correlated significantly with strong social habits in the nesting season, then it would be expected that the lack of dimorphism in *A. u. couchii* would be associated with less social habits than those of *A. u. arizonae*. And this is exactly the case, if we may judge by the brief but explicit records of observations in the literature.

Brandt (1940:18, 20, 59, 69-76) and Van Tyne and Sutton (1937:61) observed *A. u. couchii* in the Chisos Mountains of Texas.

FIG. 20 (Top).—Externally visible parti-colored bill of a postjuvenal *Aphelocoma ultramarina arizonae.*

FIG. 21 (Center).—Fledgling (approximately three weeks of age) *Cyanocitta stelleri* showing parti-colored bill.

FIG. 22 (Bottom).—Same bird as in Figure 21 (immediately above); note that postjuvenal molt has begun on forehead and the bill is almost black.

AGE DIMORPHISM IN BILL COLOR

They found nests with eggs and young and young out of the nests, and indicated nowhere that more than two adults were in attendance at any nest, though both mention the flocking habits of the species. Brandt (1940:72) states that the nests are always far apart, while Sutton and Van Tyne describe the parent birds becoming excited when the nest was approached. It is seemingly not known whether *A. u.* "*sordida*—1" has habits similar to those of *A. u. couchii,* but judging by bill color resemblances their correspondence in social habits seem probable. Moreover, I believe it is not illogical to predict that populations of *A. u. sordida* in southern Hidalgo ("*sordida*—2") that possess age dimorphism in bill color will exhibit a correlated higher degree of sociality similar to that in *A. u. arizonae,* and further that other races of *A. ultramarina* with age dimorphism of bill color are also highly social.

In *A. ultramarina* and *unicolor* it seems possible that the primitive social condition is that seen in all populations except *A. u. couchii* and probably "*sordida*—1" today. Thus the behavioral point of departure of *A. ultramarina* as a species from the "main line" of the evolution of *Aphelocoma* would have occurred when the latter was socially specialized. The change from externally visible particoloredness to virtual lack of this condition from *A. u.* "*sordida*—2" to "*sordida*—1" indicates that the locus of this change is the behavioral, morphological, and geographic point of origin of the less social branch of the species, ranging from Hidalgo north into Texas, and composing *A. u.* "*sordida*—1" and *A. u. couchii.*

In the other branch of the genus, composed of *A. coerulescens,* there is less variability in duration of age dimorphism in bill color and less variation in sociality. We have, however, seen that *A. c. coerulescens* of Florida is social at least to the point of exhibiting little territoriality and showing some evidence of helpers at the nest, although it is by no means as gregarious as any race of *A. ultramarina.* It has been postulated earlier herein that the Scrub Jay in Florida is relict, and that its habits may reflect the primitive ones of the species. Thus, we may imagine that colonization of Florida by the Scrub Jay occurred at a time in that species' evolutionary past when it was proceeding toward a lesser degree of sociality than that of the *Aphelocoma* stock at the time of origin of *A. ultramarina* but earlier than the time of origin of the "Californica and Woodhouseii groups" that all seem to be territorial.

Relationships within the "Ornate line" of New World jays.—That the Brown Jay (*Psilorhinus*) belongs in this array of other-

wise brightly colored, ornate forms is established on two bases as follows: First, *P. mexicanus* and *Calocitta formosa* hybridize in Chiapas, Mexico (Pitelka *et al.*, 1956:98-106); second, although at first glance Brown Jays are "inornate" and simply patterned, they have in fact a rudimentary, but obvious, frontal crest and a complex plumage pattern closely similar to that of most species of Cyanocorax. Figure 23 shows the heads of *Psilorhinus mexicanus* and *Cyanocorax yncas.* Note in each the malar patch continuous with a postorbital edging of the same color, the dark facial mask that proceeds over the auriculars, beneath the malar patch, and is continuous with the similarly dark throat and chest (the solid bib), and the supraorbital spot. Note the evidence in both for the uniformity of crown and nape color, which is different from the color of the back.

Age dimorphism in bill color and highly social habits of *Psilorhinus* coupled with the secondary black-billedness of *Calocitta, Cyanocorax,* and *Cyanocitta,* make it possible that *Psilorhinus* is behaviorally like the ancestor of this evolutionary line. However, it additionally seems obvious that *Psilorhinus* has "lost" its structural blue and exhibits the ancestral pattern of plumage only in different intensities of melanin.

Cissilopha may be a primitive divergent from this line, since all species of this genus exhibit distinct age dimorphism of bill color, three out of four have rudimentary crests, and, except for lack of pattern on the head (possibly obscured by melanin), all have color patterns resembling that of *Psilorhinus.* I have previously described the strong flocking nature of *C. beecheii,* and indicated that the entire genus was probably highly social.

In South America there are three species of *Cyanocorax* (*caeruleus, cyanomelas, violaceus*) forming Amadon's (1944:8) "Coronideus group" that provide an excellent morphological bridge between the remainder of the genus *Cyanocorax* and *Psilorhinus* and *Cissilopha.* These three species possess rudimentary crests, black or blackish-brown, obscurely patterned heads (visible mainly in different concentrations of melanin), and plaintipped tails. At least one, *C. violaceus,* retains the parti-colored bill well past the postjuvenal molt. In addition, there can be little question that the "Coronideus group" is closely related to the remainder of the genus *Cyanocorax,* since a fourth species, *C. cristatella* is almost perfectly intermediate, combining the robust form and blackish head of the "Coronideus group" and the white abdomen and white-tipped rec-

trices of most of the other jays of this genus. The "Coronideus group" so far as I have determined is almost completely unknown behaviorally; it would be presumptuous to assume that what little is known of the behavior of *C. dickeyi* and *yncas* would apply in any but a general way to these morphologically different South American forms. Knowledge of the natural history of the entire genus *Cyanocorax* must, it seems, be gathered before any logical

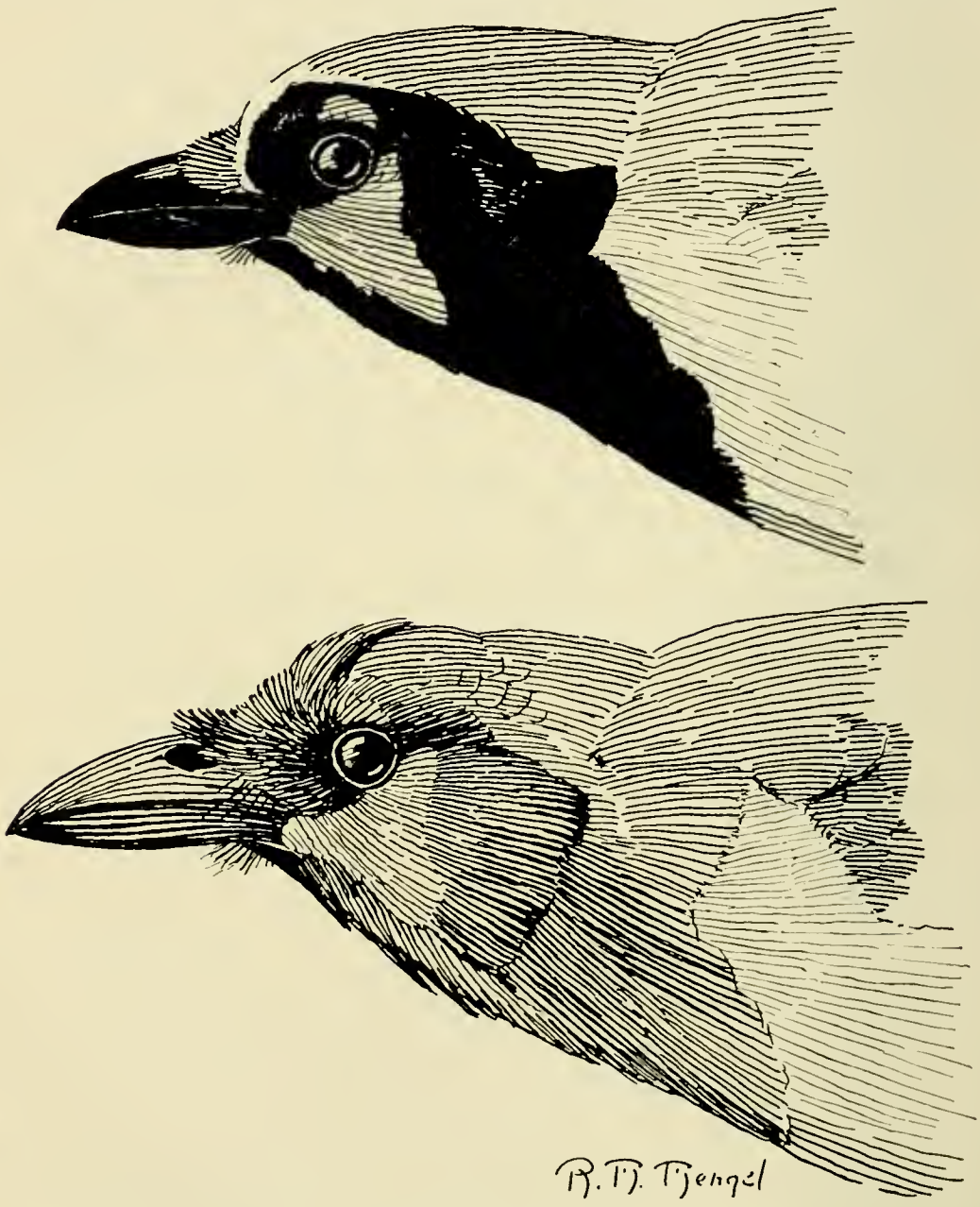


FIG. 23.—Comparison of plumage patterns of foreparts of *Cyanocorax yncas* (above) and *Psilorhinus mexicanus* (below). Note similarities in malar patch, supraorbital patch, solid-colored bib continuous with dark color of throat, auriculars and orbital region. Note also forehead of *P. mexicanus;* feathers of this region are stiff and brushy, forming a short crest.

speculation can be made as to the interrelationships between that genus and *Cissilopha and Psilorhinus.*

Cyanocitta seemingly is the farthest removed of the ornate genera from the base of the "Ornate line," having the unprecedented (in New World jays) barred feathers in wings and tail and being territorial. But for the resemblances between *Cyanocitta, Calocitta,* and *Cyanocorax,* to be pointed out later, it would be difficult to relate the former to New World jays at all. However, because of these resemblances, *Cyanocitta* seems to be most closely related to and derived from one of these two genera (more probably *Calocitta*) or from an ancestor in common with them.

Additional comments on Cyanolyca.—It has been mentioned previously that the genus *Cyanolyca* is not at this time assignable to either proposed line of evolution of New World jays. Reference has also been made to indications of low degree of sociality, under the discussion of the assumption of the primitiveness of territoriality. Now that the discussion of age dimorphism of bill color has been entertained, it is appropriate to mention again that as a whole *Cyanolyca* is characterized by no externally visible age dimorphism in bill color after early juvenal life, although parti-coloredness persists on the inside surfaces of the bill at least through juvenal life.

The previous discussion has dealt with degree of sociality and its possible correlate, age dimorphism of the bill; an attempt has been made to show the possible relationship between these factors and phylogeny of New World jays. Other characteristics were mentioned briefly and will in the following pages be discussed along with additional ones. An attempt will be made to relate these additional characteristics to the postulated phylogeny of jays.

Other Behavioral and Morphological Traits of New World Jays

Vocalizations.—The assembly and alarm calls of many species of jays seem to be the most commonly rendered by individuals of the species and the most common bases from which calls associated with more specialized behavior are derived. Thus, the *jay* of the Blue Jay, the grating *kreeup* of the Magpie-Jay, the harsh *ca! ca! ca! ca! ca!* of the Green Jay (Sutton, 1951:17), the monotonous *chow chow chow* of the Talamanca Jay (*Cyanocorax affinis zeledoni*) (Sturgis, 1928:438), the *chah chah* and *car-r-r* of *Cyanocorax cyanomelas* (Wetmore, 1926:364), the *peeah! peeah!* of the Brown

Jay (*P. morio*) (Sutton, 1951:46), the *reek* of the Mexican Jay, the *rink* of the Unicolored Jay (Pitelka, 1951:358), and the *kwesh* of the Scrub Jay are perhaps the most characteristic calls of these species.

On the basis of inflection alone, the above calls can be divided into two groups; in all except the *Aphelocoma,* the calls are downwardly inflected or uninflected, and in this genus they are upwardly inflected. This correlates directly with the two evolutionary lines postulated earlier—the "Ornate line" and the "Inornate line." Uninflected alarm or warning notes are given in rapid succession by *Cyanocorax dickeyi* (Moore, 1938:236) and *C. yncas* (Richard F. Johnston, personal communication). Upwardly inflected notes are part of the repertoire of the Magpie-Jay but are never given in alarm or assembly. I have no data on vocalizations in *Cissilopha.*

There seems to be a tendency for the development of two peculiar vocalizations in the genera *Calocitta, Cyanocorax,* and *Cyanocitta.* As mentioned earlier, these are the "pumphandle" call and the "squeaky-gate" call, which are sometimes combined (particularly in *Calocitta* and *Cyanocitta stelleri*), forming a call intermediate between the two basic ones. In *Cyanocorax,* there are two published records of each call: Amadon and Eckelberry (1955:76) describe a call of the Green Jay (*C. yncas*) as *kyompiomp*— "closer to the 'pumphandle notes' of the Blue Jay . . .," while Moore (1938:236) mentions two calls (his examples IV and V) of *C. dickeyi;* the first of these was "plaintive" given in uneasiness, the second low-pitched and musical.

Some vocalizations occur here and there throughout the garrulines and seem to be of little value in phylogenetic considerations. Such are "singing" and the rattling *br'r'r'r'r'* call. "Singing" occurs in *Calocitta* (Skutch, 1953:69, ". . . a medley of low, queer notes . . ."), in *Cyanocitta stelleri* (Bent, 1946:62), in *Aphelocoma coerulescens* (Bent, 1946:87, 100, 112, 118), and in *Cyanocitta cristata* as described earlier. The rattling *br'r'r'r'r'* call is even more widespread, occurring with seemingly little variation in quality in *Cyanocitta* (both species), *Aphelocoma coerulescens* (described in *A. c. coerulescens* as "hiccup" by Amadon, 1944b:6 and occurring also in *A. c. woodhouseii*), *A. u. couchii* (but not *arizonae,* see later), *Cyanocorax affinis zeledoni* (Sturgis, 1928:438; . . . "a very harsh metallic note like pulling a chain through a hole in a tin can."), *Garrulus glandarius* (Goodwin, 1951:420), and *Psilorhinus.* The production of the sound in the last-named genus is caused by action of air in a perhaps unique furcular pouch of the

interclavicular air sac (Sutton and Gilbert, 1942:160-5). I have never found, in cursory examination, any indication of a furcular pouch in others of the above named genera, but the sound in all these groups is so similar that it seems probable to me that the mechanisms of reproduction in each case are homologous to each other.

Trends in characteristics of plumage.—There can be little doubt that there is a tendency in the family Corvidae for the development of crests; this is particularly evident in the garrulines and in the magpies of the corvines. In, for example, the Old World *Kitta, Platysmurus,* and *Garrulus,* and the New World genera of jays, except *Aphelocoma, Cyanolyca,* and *Gymnorhinus* there are one or more crested species.

Although the presence or absence of crests seems to correlate well with other characteristics separating two evolutionary lines of New World jays, it should not be implied from this that members of the "crested" group are united by anything more than a tendency for elongate head feathers; in some cases they are not. The genus *Cissilopha* is a notable example. In the species *C. san-blasiana* there is a wholly frontal crest, composed of a few elongate, narrow feathers interspersed with many short bristly ones (according to my examination). This crest is decumbent except when actively erected and according to Pitelka (in a letter) is more pronounced in first-year birds. Ridgway (1904:312) refers to the elongate feathers especially of the pileum in *C. melanocyanea.* These form a bushy, coronally located, decumbent crest. Finally, young of *C. beecheii* according to Sutcliffe (1926:103), who kept individuals in captivity, develop an extraordinary growth of feathers standing straight up just above the eye. The crest forms at about one week of age and is lost before adulthood. In the species *C. yucatanica* there does not seem to be a crest. Thus, even within this genus of four, obviously closely related, species of jays, there are different expressions of the tendency to develop a crest; each develops in a different place, all are rudimentary, and one disappears before adulthood.

While only the tendency to develop crest feathers may in a general way indicate a relationship between species of *Cissilopha* and between that genus and other crested forms, the crests in *Calocitta, Cyanocitta,* and *Cyanocorax* are much more similar to each other. In these (three) genera, the crests are primarily fronto-coronal in origin and erect, except when actively depressed (only partially

depressable in most forms). The crest in *Calocitta* is specialized in having spatulate feathers, which are lax and plumelike, while the crest of some species of *Cyanocorax* (for example, *dickeyi*) is "tufted" into a stiff, hardly moveable, brushlike structure. The crests of all these genera may be homologous and indicate a common, crested ancestor. If this is so, the ancestor would have possessed a crest with contributory feathers extending from the frontal region to the occiput and from eye to eye, truly a monstrous adornment. Yet, one living species of jay, *Cyanocorax* (=*Uroleuca*) *cristatella of* South America possesses just such a crest according to Amadon (1944a:9), offering evidence for such an ancestor.

Color pattern seems to differentiate the "Ornate line" from the "Inornate line." In the former whitish- or yellowish-tipped rectrices occur in *Psilorhinus mexicanus, Cissilopha yucatanica* (young only), *Cyanocorax* (nine of 12 species), *Calocitta,* and *Cyanocitta cristata.* The presence of white-tipped tails in *Psilorhinus mexicanus* and absence in another otherwise closely related form, *P. morio,* their presence in *Cyanocitta cristata* and absence in *C. stelleri* points up the instability of this characteristic; but its occurrence in at least one species in each genus of the "Ornate line" indicates that development of pale-tipped rectrices, like crests, may be considered a tendency in this group of genera.

Dark bibs are characteristic of almost all species of New World jays. In the "Ornate line" these bibs vary from pale to dark but are always solid-colored. In the "Inornate line" the bibs are always streaked or broken by lighter coloration, this being evident in distinctly patterned forms such as *Aphelocoma coerulescens insularis* as well as in subtly marked forms such as *A. ultramarina;* it is not evident in *A. unicolor* (which is melanistic to a degree that almost obscures pattern.)

A basically different pattern of markings on head and neck occurs in the "Ornate line" and the "Inornate line." In the former, a complex set of black frontal, supraorbital, postorbital, supramalar, and throat markings are found; these interconnect with each other and with a bridle and the bib, which are also black. In Figure 24 it can be seen that there are two basic patterns of these head markings, but that both patterns occur within the genera *Calcocitta* and *Cyanocorax,* thus serving to link all the genera illustrated on the basis of plumage pattern of the head. It will be recalled that one of the head patterns seen in *Cyanocorax yncas* and *Calcocitta formosa colliei* occurs also in *Psilorhinus* (Fig. 23). Color pattern of the

head is obscured or absent in *Cissilopha*, of course, although occasional first-year birds show a lighter colored area on the pileum. The same obscureness or absence of pattern occurs in dark northern races of *Cyanocitta stelleri*, but in the southern races of this species a pattern similar to that in *Cyanocitta cristata* is revealed because of the lesser concentration of melanin in these southern forms.

In contrast to the "Ornate line" color pattern in *Aphelocoma* is limited to a dark facial mask and, in some races of *A. coerulescens*, whitish markings on forehead and supraorbital areas.

The genus *Cyanolyca* possesses puzzling features of plumage that make it difficult to relate to either proposed evolutionary line. Although the genus may be a natural group, it approaches in its variation both the ornate and inornate jays. *Cyanolyca nana* resembles *Aphelocoma coerulescens* (and was actually placed in that genus by Salvin and Godman, 1879-1904:407-14). *C. nana's* blackish mask, light forehead, and whitish throat particularly cause it to resemble the Scrub Jays. *C. pumilo* is completely black-throated and is like *A. unicolor* in some respects. *G. pulchra* is robust and possesses much black on the head, causing Amadon (1944a:7) to state that "*Cissilopha*" ("*Cyanolyca*"?) *pulchra* (including *cucullata* of central America and Mexico; see Miller *et al.*, 1957:120) is a link between "*Cyanolyca*" and "*Cissilopha.*" Although as Amadon states, *C. pulchra* is heavy-billed like *Cissilopha*, parti-color billedness is absent postjuvenally and the peculiar color pattern of the head is absent in at least adult plumages of *Cissilopha*. In *C. cucullata* there is a narrow white line passing above the eye posteriorly behind the cheek and down to the posterior sides of the throat and separating a wholly black face and throat from a pale blue crown and nape. *C. mirabilis* has a similar white line but is white-throated and black-capped. Most species of *Cyanolyca* are of stocky proportions, only *C. nana* and *pumilo* approaching *Aphelocoma*, for example, in slenderness of body-form. There is thus no basic pattern of plumage or of body proportions that unite the members of this genus to one another or cause them to resemble as a whole any other genus or group of genera of New World jays. The characteristics of *Cyanolyca* do not seem to uphold any generalizations or speculations thus far made in the discussion of phylogeny, but neither do they seem to make more tenuous the logic of these.

Some inter- and intrageneric considerations.—The differences discussed above in pattern of plumage and behavior between the two proposed evolutionary lines of New World jays seem to be the

most consistent ones. Certain other characteristics seem less consistent, not only in their present failure to correlate with the overall evolutionary picture of New World jays but with any system of arrangement of which I can conceive. Their present limited application or lack of correlation is without doubt owing in part to our lack of knowledge of many genera and species. For example, I am unable to find a single reference in the literature to the voice of any species of *Cyanolyca,* or of most of the species of *Cyanocorax.* Data on nests and eggs of most of the species of jays that do not occur in the United States are rare. Some of these characteristics, known for certain species, deserve consideration on a comparative level. It is hoped that the following discussion will encourage other workers to publish information of a similar kind on the less well-known species and to uncover previously published references to these that I have overlooked.

Behavior at the nest differs markedly in *Aphelocoma* and *Cyanocitta.* Except for conversation notes, the Blue and Steller's Jays are seldom vocal at or near the nest. This contrasts with the behavior of the Scrub Jay (*A. c. woodhouseii*) and the Mexican Jay (at least *A. u. arizonae* and *couchii*), which seldom exhibit any caution in approaching or leaving their nests. Individuals of the Mexican Jay in particular are prone to give loud alarm calls when approaching, leaving, and frequently while sitting on the nest.

Jays of the genera *Cyanocitta* and *Calocitta* possess great manipulatory ability with the tongue; this ability is absent in *Aphelocoma ultramarine arizonae.* The development of this facility in other species of jays seems to be undocumented.

Flight display in courtship of the Blue Jay and the Magpie-Jay is identical (Fig. 3). In both species, individuals fly slowly with the tail spread and wings extended with the primaries fanned from the wrist. No such display occurs in *Aphelocoma ultramarina arizonae* or *A. coerulescens woodhouseii.*

Differences between *A. u. arizonae* and *A. u. couchii* in sociality and age dimorphism in bill color have been discussed. There are other differences between these two subspecies further emphasizing the possible existence of two behavioral groups in the species (the "Wollweberi and Ultramarina groups" together with *A. u. "sordida*—2" on the one hand and *A. u. couchii* and "*sordida*—1" on the other). *A. u. arizonae* lays unspotted eggs, while *A. u. couchii* lays spotted ones (as do most jays). According to Brandt (1940:72) *A. u. couchii* lines its nest with horsehair, while *A. u. arizonae*

never uses hair but instead lines its nest with rootlets, although such hair is available and more plentiful (according to Brandt) in the range of the latter race than in that of the former. Lastly, vocalizations of these two races are different. Impressive is the presence of the rattling *br'r'r'r'r'* call in *A. u. couchii* (Brandt, 1940:

FIG. 24.—Plumage patterns of foreparts of jays of the "Ornate line." *a. Cyanocitta cristata; b. Calocitta formosa azurea; c. Calocitta formosa collei; d. Cyanocorax dickeyi.* Note that the different patterns in two subspecies of *Calocitta formosa* (*b.* and *c.*) resemble the patterns in *Cyanocitta* (*a.*) and *Cyanocorax* (*d.* and *e.*), respectively.

75, who likens it to a similar call of the Blue Jay) and its total absence in *A. u. arizonae.* In addition the assembly and alarm calls of *A. u. couchii* are to Brandt (1940:75) different from those of *A. u. arizonae.* Those of the former are always high-pitched and given in series of three to six. Brandt describes the call as *"oint oint oint."*

There is one habit in the nesting behavior of *Cyanocitta* that is not found in the habits of other New World jays so far as known. Both species of *Cyanocitta* use mud as a constituent of their nests. This is disconcerting in light of the postulation that *Cyanocitta* is of New World origin, because members of only one other genus of jays have been recorded as having this habit. According to Witherby *et al.* (1938:33), *Garrulus g. glandarius* uses "a little earth" in the nest. This might cause us to re-evaluate the fact that both *Cyanocitta* and *Garrulus* are also crested and possess barred feathers in wings and tail, if it were not for the fact that Goodwin (1956:202) has examined scores of nests of *Garrulus* without ever finding earth in any of them. Goodwin is of the opinion that earth in the nests of these jays got there by accident. Since Witherby (1938) is normally a highly authoritative source, the question is technically open, but it ought to be easily resolved. If *Garrulus* uses mud in nest-building, it calls for additional consideration of the phyletic relationship between *Garrulus* and *Cyanocitta.* In the meantime, however, *Cyanocitta* is at least unique in this respect among jays thought to be of New World origin, and the mutual and exclusive possession of this habit by *C. stelleri* and *cristata* should help enforce the status of the genus *Cyanocitta.* Table 2 is a comparative summary of the behavioral and morphological traits of New World jays presented in the preceding discussion of phylogeny.

Discussion and Conclusions

It will be recalled that Amadon's classification of the corvids combined as *"Cyanocitta"* the current genera *Cyanocitta, Aphelocoma, Cissilopha,* and *Cyanolyca,* of previous authors. Now it can be seen, in part on the basis of the preceding discussion and in part upon any sort of superficial examination of these and other New World groups, that each of these taxa is of meaningful, if not generic, status. That is, their current status as genera has meaning, but their combination into one genus and separation into sub-genera could also retain meaning. However, Amadon (1944a: 1) as the only worker recommending their "lumping" has objected to their

division into subgenera as follows: "Some might prefer the use of subgenera for certain of the lesser groups. Since subgeneric names are indistinguishable in form from generic ones, use of the former, as Dunn . . . recently pointed out, seems to tempt later authors to elevate them to generic status." This, however, is not a fault of subgenera, but of a few taxonomists and should not be employed as an excuse to eliminate subgeneric usage. The philosophy of present-day systematists provides little reason for such caution.

Considering what is known of the behavior and morphology of New World jays compared to what is not known of these subjects, it seems to me that any extensive adjustment (either "lumping" or "splitting") of the currently recognized genera and species at this time would be premature and might lead only to complications in the taxonomy and synonomy of these birds when further information is amassed and evaluated.

It seems clear to me that one taxonomic adjustment can be recommended at the present time: I propose that the hierarchical category of Tribes be erected in New World jays and that two such tribes, Cyanocorini and Aphelocomini corresponding, respectively, to the "Ornate line" and "Inornate line" as described in this paper, be recognized. The limits of these tribes would be as follows:

Subfamily Garrulinae
  Tribe Cyanocorini
    Genera 1. *Cyanocorax*
           2. *Psilorhinus*
           3. *Cissilopha*
           4. *Calocitta*
           5. *Cyanocitta*
  Tribe Aphelocomini
    Genus 1. *Aphelocoma*

Some workers might recommend that the "Coronideus group" of *Cyanocorax,* particularly such a form as *C. violaceus,* is, at least morphologically, excellent grounds for uniting *Psilorhinus* and perhaps *Cissilopha* with *Cyanocorax* as a single genus. These morphological (and indications of behavioral) similarities are clear. It will be clear in figure 26 depicting a hypothetical phylogeny of Cyanocorini that on the basis of existing data, I consider *Psilorhinus* and *Cissilopha* as having more recent common ancestors with the "Coronideus group" of *Cyanocorax* than the latter group does with the remaining living forms of its genus. Recognition of the relationship of the "Coronideus group" to other species of *Cyanocorax* is due for the most part, after all, to the existence of the species *C.*

Kinds of Jays	Characteristics (underlined categories not used to compute index for species)	Bill not exteriorly parti-colored in postjuveniles	Crest	Barred feathers	Solid-colored bibs	Head color pattern complex (bridle, etc.)	Spotted eggs	Pale-tipped retrices	"Pumphandle," "squeaky-gate" calls	Song	Inflection of alarm assembly calls downward or uninflected	Rattling br'r'r'r' call	Not highly social	No helpers at nest	Intermediate sociality	Territoriality or low sociality	Builds false or symbolic nest	Secretive attitude at nest	Uses mud as constituent of nest	Manipulatory facility with tongue	Index of similarity to Cyanocitta cristata
CYANOCITTA CRISTATA	X	X	X	X	X	X	X	X	X	X	X	X	X	O	X	X	X	X	X		100
CYANOCITTA STELLERI	X	X	X	X	X	X	O	X	x	X	x	X	x	O	X		x	x	X		94
CALOCITTA FORMOSA	X	X	O	X	X	x[A]	X	X	x	X		X	x/o	X				O			77
CYANOCORAX (one or more species except those included below)	X	X	O	X	X	X[B]	X	x		x	x	x	o	x	o			O			77
CYANOCORAX YNCAS	X	x/o[C]	O	X	X	x[D]	X	x		x		x		o	x			O			82
CYANOCORAX ("Coronideus group")	o	X	O	X	1	x[E]	O			x											57
CISSILOPHA	O	X	O	X	1	x[F]	X[2]			X		O		O	O						63
PSILORHINUS	O	x	O	X	x	x[G]	X[2]			X	x	o	o	o	o			O			58
APHELOCOMA C. COERULESCENS	X	O	O	O	O	x	O	o	x	o	x	x	x/o	x	o		o	o			33
APHELOCOMA C. REMOTA, SUMICHRASTI	X	O	O	O	O		O														17
APHELOCOMA C. WOODHOUSEII[3]	X	O	O	O	O	x	O	O	O	O	X	X	X	O	X		O	O			33
APHELOCOMA ULTRAMARINA ARIZONAE[4]	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	x	O	O	O		6
APHELOCOMA U. COUCHII[5]	X	O	O	O	O	x	O	O	o	o	x	x	x	x	o			O			36
APHELOCOMA UNICOLOR	O	O	O		1 O		O					o		o	o						0
CYANOLYCA (symbols denoting habits refer only to C. pumilo)	X	O	O	O	x/o		O					x			x						29

TABLE 2.—A comparative table of morphological and behavioral characteristics of some New World jays. The index of similarity in the far right column of the table is for each species the number of characteristics in which it agrees with *Cyanocitta cristata* divided by the total number of characteristic-categories in which information was available for the species. The Blue Jay was used as the basis for comparison because positive information for each category of the table was available for that species. The indices cannot be interpreted absolutely literally but can serve only as a general indication of similarity. Different forms of the basic symbols employed (X's = possession of characteristic, O's = absence of characteristic) as well as combinations of these and additional marks indicate types of source of information or special conditions as follows: X or O = indication from personal observation plus literature or personal communication with reliable source; X or O = personal observation; x or o = literature or other reliable source; x/o or other such combinations = evidence for variability as regards this characteristic. Supra-script letters in the table refer to citations (below) for characteristics which have not been referred to specifically in the text for the species in question.

[A]Skutch (1953:70); [B]Allen (1905:290), for *Cyanocorax affinis*: Moore (1938:236), for *C. dickeyi;* [C]Hellmayr (1934:32), for *C. yncas galeata;* [D]Sennett (1877:30), for *C. yncas;* [E]Cherrie (1916:212), for *C. violaceus;* [F]Suttcliffe (1926:102) for *Cissilopha beecheii;* [G]Skutch (1935:262), for *Psilorhinus mexicanus.*

1. The intensity of melanic pigment in these forms is thought to obscure all evidence of plumage pattern of the foreparts, as such pigment almost does in *Psilorhinus* and *Cyanocitta stelleri.*

2. White-tipped rectrices occur in only one species of these genera, but since the species in each case is similar to its congeners, the characteristic is here listed for the genus rather than erecting a separate category for one species bearing the characteristic.

3. Characteristics noted here for *A. c. woodhouseii* probably apply to all races of the "Californica and Woodhouseii groups" of the species.

4. Characteristics noted here for *A. u. arizonae* probably apply to all members of the "Ultramarina and Sordida groups" of the species except as noted in foot-note 5.

5. Characteristics noted here for *A. u. couchii* probably apply to *A. u. "sordida*—1" (see text).

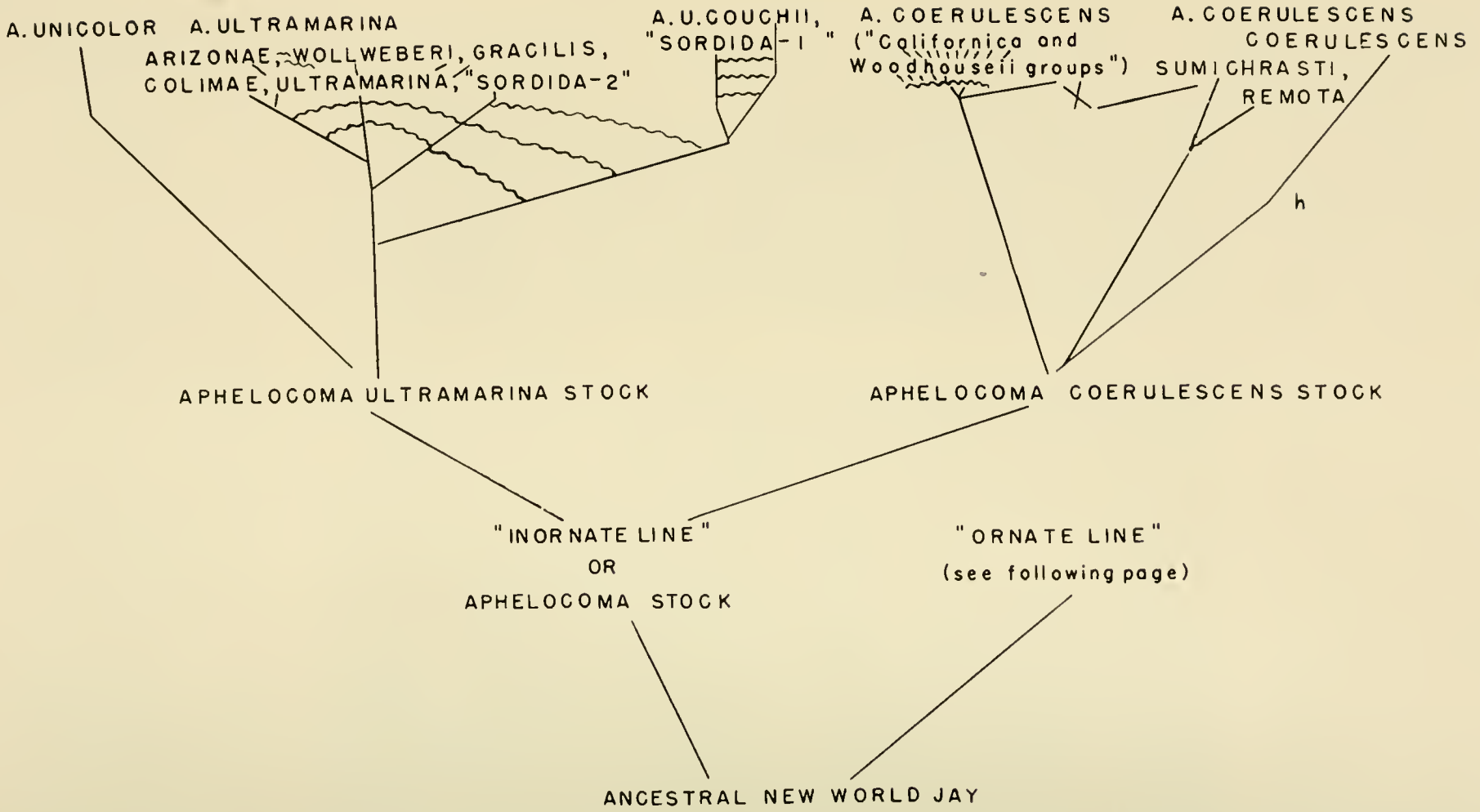


FIG. 25.—Proposed phylogeny of the "Inornate line" of New World jays, tribe Aphelocomini. Wavy lines indicate that racial intergradation occurs between races connected by these lines. There is limited evidence for intergradation between *A. coerulescens cyanotis* ("Woodhouseii group") and *A. c. sumichrasti* ("Sumichrasti group"); this possibly represents secondary contact between these two subspecies groups.

cristatella. However, the special social nature of *Psilorhinus*, and the fact that behavior of most species of *Cyanocorax* is poorly known, makes an actual recommendation for taxonomic alterations of these three genera seem unwise to me at this time.

Although I have not placed *Cyanolyca* in the above tribal classification, there can be no doubt that it does belong therein and perhaps unites the two tribes. Its morphological affinities seem to be more with the Aphelocomini than with Cyanocorini, but because of almost complete lack of knowledge of behavior in the genus, there can be no choice but to await further study before assigning it a place in the classification.

Figures 25 and 26 depict the hypothetical evolutionary relationships of the genera of jays here discussed, as conceived at this time. Footnotes to figure 26 summarize evolutionary events that have possibly occurred in the "Ornate line" based on morphological and behavorial data discussed above.

SUMMARY

Studies on behavior and phylogeny of New World jays are described in this paper.

Differences in courtship and reproductive behavior of species of jays seem to be correlated with differences in sociality. Courtship in the Blue Jay (*Cyanocitta cristata*) consists of three stages, group courtship, courtship feeding, and false nestbuilding. The Mexican Jay (*Aphelocoma ultramarina arizonae*) is a highly social race, and thus, although courtship feeding and false nestbuilding occur, all the members of a flock participate in these activities. True nestbuilding is, in this race, a part of courtship.

In the Blue Jay, true nestbuilding arises from false nestbuilding; both members of the pair participate in building the true nest. Blue Jays are territorial, the behavior first being expressed after nestbuilding is commenced. Both members of the pair build the nest.

The Mexican Jay in Arizona is not territorial and has narrow ecologic requirements; the Scrub Jay (*Aphelocoma coerulescens*) throughout most of its range is territorial and can live in much poorer (more xeric) areas than does the Mexican Jay. Nonterritorial Scrub Jays in Florida have less ecological adaptability than the rest of the species. Lack of territoriality may thus be an adaptation to restricted ecologic adaptability.

In the Blue Jay copulation occurs after *Nudging* display in the late stage of nestbuilding. Only the female of the pair, there-

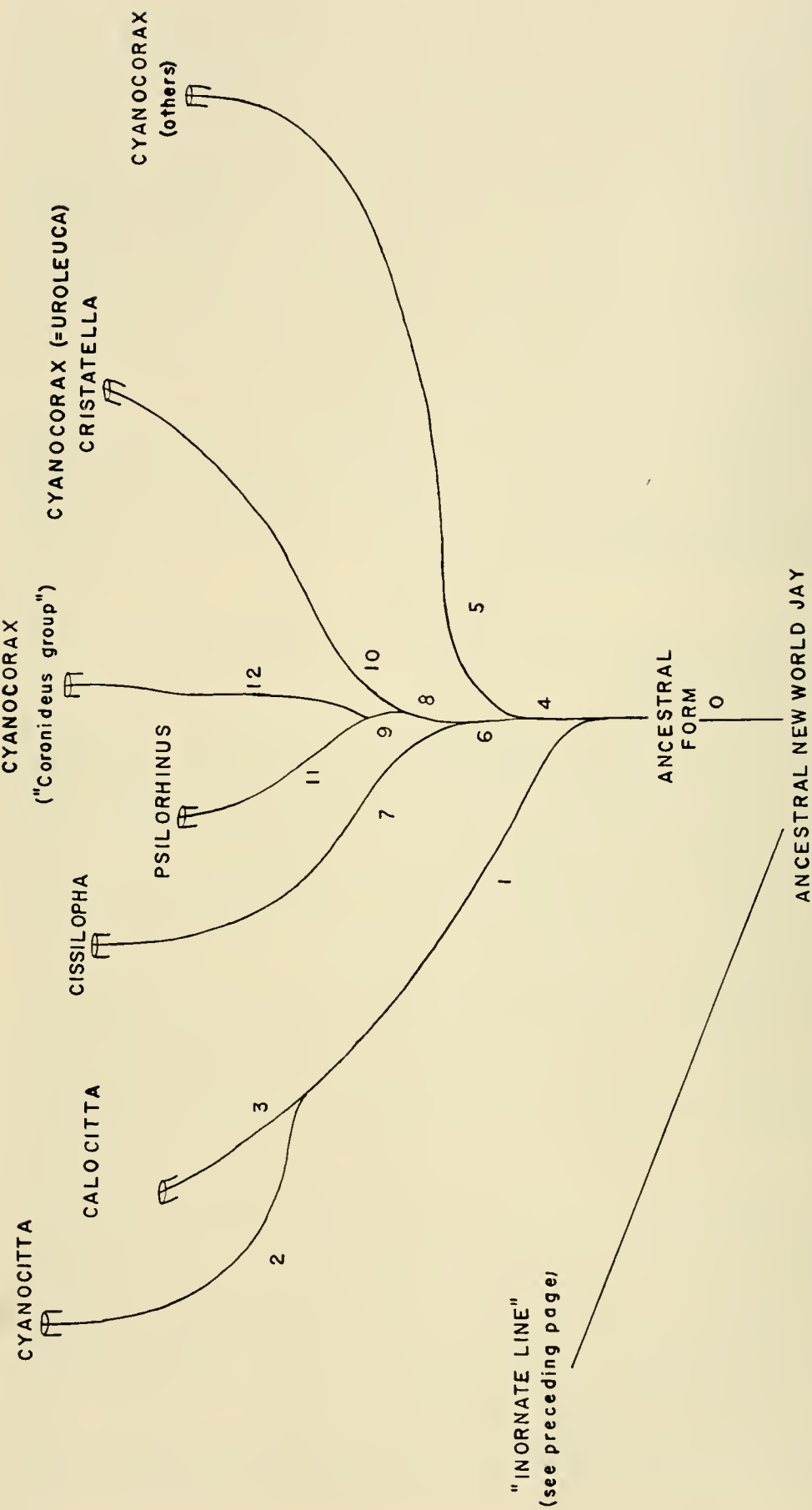


FIG. 26.—A hypothetical phylogenetic tree of the "Ornate line" of New World jays, Cyanocorini. The present diagram is three dimensional, so that groups indicated by names at ends of lines are all living. Numerals refer to corresponding footnotes that explain supposed morphological and behavioral trends in each proposed evolutionary line.

0. Highly social; robust form; prolonged age dimorphism in bill color; short crest covering frontal, coronal, and occipital regions of head; basic color pattern of foreparts as illustrated in figure 24; tropical distribution.

1. Becoming less social; losing age dimorphism of bill color; developing elongate crest; spreading northward and out of tropics.

2. Becoming territorial; losing postjuvenal parti-coloredness of bill; becoming smaller in size and less robust in form; developing barred plumage; entering temperate and boreal regions; secondarily entering southern latitudes via mountains of Mexico (*C. stelleri*).

3. Retaining intermediate sociality; losing postjuvenal parti-coloredness of bill; (but retaining this parti-coloredness inside the bill longer than *Cyanocitta*); retaining large robust form; inhabiting subtropical regions, western and southern Mexico.

4. Retaining sociality; retaining prolonged age dimorphism of bill color; possessing the short, extensive, ancestral form of crest; retaining large, robust form; tropical middle latitudes.

5. Becoming more ornate—elongate upright crest in most forms and vividly contrasting color pattern; losing postjuvenal parti-coloredness of bill; spreading over northern South America and north in Mexico in subtropical mountain forests, semi-arid scrub.

6. Retaining sociality; remaining relatively inornate; retaining short but extensive crest; remaining tropical in distribution in middle latitudes.

7. Retaining sociality; retaining prolonged parti-coloredness of bill; remaining robust; losing extensive crest (crest highly variable); spreading northward to subtropical Mexico and mountains of central America.

8. Retaining sociality; retaining prolonged parti-coloredness of bill; robust form; retaining short, extensive crest; remaining tropical.

9. Remaining social; prominent age dimorphism of bill color persisting; remaining tropical in middle latitudes but spreading northward also.

10. Socially unknown; prolonged age dimorphism of bill color lost (?); retaining robust form; crest both extensive and elongate-recurved; inhabiting tableland of Brazil (Hellmayr, 1934:30).

11. Remaining social; retaining prolonged age dimorphism of bill color; losing crest except frontally; losing structural blue coloration (becoming brown), thus revealing basic color pattern of foreparts; spreading north into central America and Mexico, remaining tropical.

12. Degree of sociality unknown; retaining prolonged parti-coloredness of bill color; losing crest except frontally; not losing structural blue coloration; remaining tropical in South America.

after, occupies the nest in egg-laying and incubation. The male remains close by and occasionally feeds his mate.

In the Mexican Jay, the female performs incubation and is attended both by her mate and by other members of the flock. Compared to Blue Jays, Mexican Jays are not secretive when near the nest.

Male and female Blue Jays feed the young. After the young leave the nest, territoriality is abandoned and the adults follow the young wherever they go. Feeding of the young continues until about the time of postjuvenal molt.

Young Mexican Jays are cared for by their parents and by other members of the flock.

Compared to young Mexican Jays, young Blue Jays and Steller's Jays have greater manipulatory facility with the tongue, bathe and preen more frequently, and have a greater variety of vocalizations. Young Blue Jays sing frequently after postjuvenal molt commences; young Steller's and Mexican Jays raised in the course of this study did not sing.

Although Blue Jays flock in autumn, these flocks are not closely integrated as in Mexican Jays; individual distance is maintained. Migration is characteristic of first-year Blue Jays; many adults do not migrate. Winter territories or feeding areas seem to be maintained by Blue Jays, and food-storing may function as a spacing mechanism in winter.

Mexican Jays do not migrate, the flocks remaining on foraging and breeding areas the year around. Food-storing seems not common in Mexican Jays in the wild, but is frequent in captive individuals.

Mobbing by Blue Jays is preceded by several stages of behavior as follows: curiosity, anxiety, "identification," and "realization" of danger. Usually only two birds (members of a pair) attack a predator. Contact with the predator occurs.

In the Mexican Jay, all members of the mobbing flock react alike (unless the predator is near a nest).

Mexican Jays in captivity form a peck-order. In four captives studied by me, the order was straight line and established by peck-dominance. Males dominate females and black-billed adults dominate subadults, which have parti-colored bills. The age relationship prevails over the sexual relationship. Thus, an adult female may feed a young male in captivity. A ritualized series of behavioral events is involved in expression of peck-dominance. These

events include pecking by both birds at the tarsi, wings, and head of the opponent.

There seem to be two phylogenetic lines of jays of New World origin; these may be termed the "Ornate line" and the "Inornate line." *Aphelocoma* is the sole genus in the latter line, although *Cyanolyca* may belong therein. It is here proposed that degree of sociality and the characteristics of dimorphism of bill color and rate of sexual maturation are correlated. It is speculated that a high degree of sociality is primitive, since less sociality and loss of prolonged external parti-coloredness of the bill are correlated. In less social species parti-coloredness is evident in postjuvenal birds and is retained on the inside surfaces of the bill thereafter for a variable period.

In the "Inornate line" many Mexican races of the Scrub Jay and Mexican Jay and the species *A. unicolor* are poorly known behaviorally, but from what is known, it seems that low sociality has arisen independently in the Scrub and Mexican Jays. The lack of strict territoriality and occurrence of helpers at the nest in the isolated Florida Scrub Jay indicate that this relict race may represent the primitive condition of the species in these respects. In addition, in the species *A. ultramarina,* the races *couchii* and *sordida* (but only in part) may be less social than the remainder of that species and *A. unicolor.* If age dimorphism in bill color is correlated with sociality, transition from high sociality to low sociality occurs within the race *A. u. sordida* from southern Hidalgo, Mexico, northward, toward the range of *A. u. couchii.*

Because of lack of information on behavior, relationships in the "Ornate line" are particularly obscure, but it seems that in habits *Psilorhinus* is primitive, although it is specialized morphologically and not ancestral to others of the "Ornate line." A basic color pattern of the foreparts is shown to be common to most members of the "Ornate line." The "Coronideus group" of *Cyanocorax* serves to "unite" morphologically *Psilorhinus* and *Cissilopha* and other species of *Cyanocorax.* Many behavioral and morphological characteristics are shared by *Cyanocorax, Calocitta,* and *Cyanocitta,* the latter genus possibly being most closely related to *Calocitta* among living jays.

Two tribes are proposed as useful taxonomic categories in New World jays; these tribes, Aphelocomini and Cyanocorini, correspond to the "Inornate line" and the "Ornate line," respectively.

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Some Morphological and Functional Aspects of Certain Structures of the Middle Ear in Bats and Insectivores

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ABSTRACT: A detailed morphological study of the tympanic membrane, auditory ossicles and intra-aural muscles was undertaken in three genera of insectivores and eight genera of bats in the hope of correlating these structures with the frequencies of sound known or presumed to be utilized by the various forms. In the forms investigated there are strong suggestions that size, attachments and other morphological features may be of considerable significance in high frequency and ultrasonic perception.

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INTRODUCTION

In the past twenty-five years considerable information concerning ultrasonic vocalization by bats has been gathered. Griffin's (1958) treatise and the work of Novick (1958a; 1958b) provide an account of the current concepts of this subject and, also, an excellent critique of earlier works. It now seems to be well established that Microchiroptera utilize self-omitted high frequency sound waves as a means of orientation, obstacle avoidance and food gathering; this phenomenon is known as echolocation. With the accumulation of physiological information along these lines, an interest in morphological mechanisms responsible for the reception and transmission of high frequency sound is developing. To date only a few anatomical investigations have been undertaken in connection with physiological findings; for the most part, these have been restricted to the inner ear. Studies on the cochlea in bats have shown that it is typically mammalian in its basic structure, but, in some forms, it shows structural peculiarities in those parts concerned with high frequency hearing (Iwata, 1924; Ikeda, Yoshindo and Yokote, 1939).

The auditory ossicles and the intra-aural muscles in many mammalian forms have been subjected to morphological study (Doran, 1878; Cockerell, Miller and Printz, 1914a, 1914b; Wassif, 1948, 1950). Investigations along these lines tend, however, to be relatively superficial and incomplete in detail; this coverage has apparently sufficed for taxonomic problems, which have constituted the major stimulus for these studies.

A rather exhaustive search of the literature has, however, failed to disclose any comprehensive interpretations of the functional morphology of the middle ear in lower mammalian forms.

This investigation was undertaken with the hope of accomplishing several results: 1) to survey and describe the middle ear in some representative insectivores and bats; 2) to attempt a correlation of structure and function with frequency ranges presumed

to be used by the various forms; and 3) to augment morphological and functional information concerning the mammalian middle ear.

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MATERIALS AND METHODS

Specimens used in this investigation were provided by the Museum of Natural History, University of Kansas, or were collected personally. The forms studied are listed below; those from the Museum of Natural History are designated "KU" and their catalogue numbers are listed.

Order Insectivora
- Family Erinaceidae
  - *Erinaceus europaeus*
- Family Soricidae
  - *Cryptotis parva*
- Family Talpidae
  - *Scalopus aquaticus*

Order Chiroptera
- Family Rhinolophidae
  - *Rhinolophus ferrum-equinum nippon*—KU 64415
- Family Phyllostomatidae
  - *Glossophaga soricina*—KU 19403, 19404
- Family Natalidae
  - *Natalus mexicanus*
- Family Vespertilionidae
  - *Myotis velifer*
  - *Eptesicus fuscus*
  - *Plecotus townsendii*—KU 82217
- Family Molossidae
  - *Tadarida brasiliensis*—KU 82218
  - *Eumops perotis*

Gross dissections and studies of serially sectioned heads were the primary methods utilized in this investigation. The usual histological techniques employed for serial sectioning and staining

proved unsatisfactory because of the density of bone in heads of adult animals, and because of the thickness of the sections (80 microns) which were desired. A method was devised, however, which has proved quite satisfactory and reliable.

The heads were removed from freshly killed, or formalin fixed, specimens and placed in Bouin's picroformol for several weeks. After fixation the heads were rinsed in water and then decalcified for 10-24 hours in an electrodecalcifier (Lab-tronics, Inc.); the end-point of decalcification was determined radiographically. After complete decalcification the heads were washed in running water for approximately one hour, and then run through a standard alcoholic dehydration series, up to 95% alcohol. While in a second change of 95% alcohol, the heads were placed into a vacuum chamber in which negative pressure equivalent to 25 inches of mercury was produced over a period of from 8-24 hours. The specimens were kept at this pressure until bubbles ceased to rise from the tissues, and the specimens rested on the bottom of the container rather than tending to float. Pressure was then slowly returned to normal.

After two changes of iso-amyl acetate (24 hours) the heads were infiltrated with a 10% solution of Hercules Low Viscosity Nitrocellulose (R.S. ½ second) for two or three days, depending on the size of the specimens. Subsequent infiltration with 15, 20, 25, 30 and 35% nitrocellulose solutions followed for periods of 4, 6, 12, 18 and 27 days, respectively.

The infiltrated heads were blocked for sectioning in 35-40% nitrocellulose, using molds constructed of filter paper. Three changes of chloroform, each of 24 hours duration, were generally necessary to harden the blocks sufficiently. After hardening, the blocks were transferred to a solution consisting of three parts 95% alcohol and one part glycerin. After two or three days in this solution, the blocks were generally ready for sectioning, but could be stored in the glycerine-alcohol solution indefinitely.

The heads, embedded in their nitrocellulose blocks, were sectioned on a sliding microtome in the usual manner. Sections were affixed to slides in accordance with the glycerine-alcohol technique described by Bensely and Bensely (1938:64), and stained using the Mallory (1938) technique. Superior differentiation was obtained in thick sections ranging up to 90 microns if they were stained for approximately one minute in solution I (acid fuchsin 0.5 gm, distilled water 100 cc) and approximately two minutes in solution II

(0.5 gm aniline blue, 2 gm orange G, 1 gm phosphotungstic acid and 100 cc distilled water), and, then, were allowed to differentiate in tap water before being placed into 95% alcohol. Differentiation was stopped by placing the slides in absolute alcohol.

Dissections, used in conjunction with the serial sections, were executed at magnifications ranging from nine to 30 diameters. The area of the tympanic membrane was determined by measuring its long and short diameters with a calibrated ocular grid and, subsequently, calculating according to mathematical formulae. The value thus obtained does not correspond to the total area, since the membrane is somewhat concave in all forms. The area of the vestibular surface of the footplate was calculated by counting the number of squares of the ocular grid occupied by the footplate, then multiplying by an appropriate constant. Volumetric measurements of the ossicles and intra-aural muscles were determined in serial sections by counting the number of squares of the grid which covered the sections through the ossicles and the muscles. The total number of squares counted was multiplied by the area of each square, and the value obtained was multiplied by the thickness of the sections; all measurements were calculated in millimeters. Since measurements were carried out on only one or two specimens of each species, and since the ages of the specimens were not known, these measurements can not be considered average representative values for adults of the various species. Each specimen, however, appeared to a mature adult.

BASIC MORPHOLOGY AND NOMENCLATURE OF THE MIDDLE EAR IN INSECTIVORES AND BATS

In the forms considered, the morphology of the middle ear follows the general mammalian organization, but is subject to considerable variation in detail. Even in relatively "primitive" forms, such as insectivores and bats, certain parts and processes show modifications, some of which appear to be related to changes in auditory mechanisms; other modifications seem to bear no detectable relationship to hearing. Despite these variations, a basic pattern is present. A description of this pattern seems appropriate in that it will serve to establish the nomenclature used, and will eliminate undue repetition in descriptions of specific forms.

The *middle ear* (auris media) may be said to consist of a *tympanic cavity* (tympanum) and its extensions, and the structures forming, suspended within, or associated functionally or passively with these spaces.

The tympanic cavity is the entire air-filled space, lined with mucous membrane, and enclosed by the various membranous, cartilaginous, and bony walls that bound it; it lies between the *external ear,* and the *inner ear.* It communicates with the pharynx by way of the *Eustachian* (auditory, pharyngeotympanic) *tube,* and suspended within it are parts of the auditory ossicles, the intra-aural muscles, and segments of the chorda tympani nerve and stapedial artery. The two major divisions of the tympanic cavity are the *tympanic cavity proper* and the *epitympanic recess.* The former is an ill-defined area lying between the tympanic membrane and the *labyrinthine wall,* which is formed by the outer wall of the petrosal bone; it contains all of the major structures of the middle ear, except the head of the malleus and the body of the incus. The epitympanic recess is a dorsal extension of the tympanic cavity which lies above the upper level of the tympanic membrane. Contained within it are those parts of the malleus and incus which articulate to form the *incudomalleolar articulation.* Posterior to (but in close association with) this recess is the *fossa incudis;* it contains the short process of the incus and its walls provide an area for the attachment of the posterior incudal ligament.

The mucous membrane (tunica mucosa tympanica) lining the tympanic cavity envelops or covers all structures of that cavity. It is reflected onto the ossicles and helps suspend them by means of thickenings over the head of the malleus and body of the incus, which form the so-called *suspensory* (superior) *ligaments* of the malleus and incus. Extensions of these membranous reflections may continue along the short process of the incus as an *incudal fold* (plica incudis); reflections onto the anterior process of the malleus constitute an *anterior malleolar fold* (plica malleolaris anterior); a similar reflection onto the manubrial base and/or orbicular apophysis constitutes the *posterior malleolar fold* (plica malleolaris posterior); and an extension from the posterior wall of the tympanic cavity to the stapes forms the *stapedial fold* (plica stapedis). Mucous membrane also covers the inner, *tympanic surface* of the tympanic membrane and the outer, *tympanic surface* of the *secondary tympanic membrane* (membrane of the fenestra cochleae). In certain areas membraneous pouches or sacs are formed; these may invade the walls of the tympanic cavity to form pneumatized areas which, in some forms, become ossified and form bony *tympanic cellulae.*

Although many different elements may form the walls of the

tympanic cavity, the *petrosal bone, tympanic bone* and the tympanic membrane are constant boundaries of this cavity. Since the total morphology of the petrosal bone does not seem pertinent in this investigation, only those of its parts which serve as landmarks are considered here.

The petrosal bone forms the medial, or labyrinthine, wall of the tympanic cavity. This wall frequently shows the outline of the entire lateral surface of the cochlea, or only its basal whorl may be outlined and form a bulging prominence, the *promontory.* A depression in the promontory, the *fossula fenestrae vestibuli,* leads to an oval foramen, the *fenestra vestibuli* or *ovalis.* Within the fossula are the crura of the stapes, which unite with the footplate of the stapes and form the boundaries of the intercrural foramen of the stapes; traversing the outer portion of the fossula and passing through the intercrural foramen, is the stapedial artery. The footplate of the stapes occupies the fenestra vestibuli and is held in place by the annular ligament. Posterior to the vestibular fossula is a second depression, the fossula fenestrae cochleae, which houses the fenestra cochleae (round window); this is covered by the *secondary tympanic membrane,* which occupies the depths of the fossula. Near the anterior border of the petrosal bone is a shallow longitudinal fossa, which extends posteriorly almost to the margin of the fossula fenestrae vestibuli; this marks the position of the tensor tympani muscle and is called the *fossa of the tensor tympani.* The labyrinthine wall is also marked by arterial grooves formed by the artery of the promontory and the stapedial artery.

The tympanic bone (Fig. 1) provides an area of attachment for the pars tensa of the tympanic membrane. It is always present, but varies considerably in form; it may occur as a separate element, it may be partially fused to surrounding bones, or it may merge completely with them and be indistinguishable as a separate element. The morphology of the tympanic bone has received extensive treatment by Van der Klaauw (1931). It is often termed ectotympanic, annulus tympanicus, tympanic ring, or just tympanic. In many mammals this element is a narrow, incomplete ring, a condition usually signifying primitiveness (Van der Klaauw, 1931). In more specialized forms the tympanic bone tends to be expanded medially and/or laterally to form a bony ventral covering of the tympanic cavity and/or part of the external auditory meatus, respectively. (The term *auditory bulla* is often used in reference to this basal covering of the auditory region. The mammalian bulla,

however, is exceedingly variable and may be formed by many different bony elements; it may be formed entirely by the tympanic; it may incorporate any or all of the adjacent skeletal elements; it may be cartilaginous, membranous, bony, or any combination of these. The term *auditory bulla* will, therefore, be avoided in this paper except where it is necessary to refer to investigations of others.)

The shape of the tympanic bone is usually described as "ring-like" or "horseshoe-shaped"; the *tympanic notch* (incisura tympanica, incisura of Rivinus), the opening between the tips of the two legs of the tympanic bone, varies considerably in size in different forms. The size of the notch is dependent upon the curvature of the two legs, and upon the extent to which they approach one another. The two legs, anterior (rostral) and posterior (caudal), usually incline posteriorly and are directed dorsally, laterally, or in a combination of these directions.

On the anterior surface of the anterior leg there is a shallow depression, the *sulcus malleolaris,* with which the tympanic plate of the malleus articulates, or becomes fused. As a rule the two legs are attached to the squamosal bone on the anterior and posterior parts of the *margo tympanica squamosi;* the petrosal bone, however, is often involved (Van der Klaauw, 1931). The attachment of the tympanic legs to these bones may be accomplished by a synchondrosis (cartilaginous ankylosis), a synarthrosis (fibrous ankylosis), or by a synostosis (osseous ankylosis).

Circumscribing the inner surface of the tympanic bone, and extending along each leg, is a groove, the *sulcus tympanicus.* Along the medial margin of this groove is a crest, the *crista tympanica* (Bondy) or the *margo sulci tympanica* (Van Kampen). The sulcus tympanicus and/or the crista tympanica provide an area of attachment for the annulus fibrosus of the tympanic membrane; this annulus may attach to the sulcus exclusively, to the sulcus and the lateral border of the crista, or entirely to the crista. In association with the distal extent of the crista, on each leg of the tympanic bone, two spines may occur; the *spina tympanica anterior,* a spine on the inner surface of the anterior leg, represents the anterior limit of the crista; on the posterior leg, the *spina tympanica posterior* represents the extent of the crista. The lateral margin of the sulcus tympanicus is usually continuous with a lateral expansion of the tympanic bone, which, when present, forms the *recessus meatus acousticus externi* (or recessus meatus) and con-

tributes to the floor of the external auditory meatus. Medial to the crista tympanica there is usually an expansion of the tympanic bone that forms part of the ventral floor of the tympanic cavity; the term *bulla tympanica* is best applied to this medial expansion of the tympanic bone. In many forms the bulla tympanica does not extend medially as far as the medial wall of the tympanic cavity. The intervening area may be closed over by connective tissue, or by elements falling under the classification of *entotympanic.* Under this name, Van der Klaauw (1931) considers all skeletal elements, bony or cartilaginous, which lie in the ventral wall of the tympanic cavity, and which are primarily independent of other bony elements in the auditory bulla, except perhaps the tympanohyal and the cartilage of the Eustachian tube.

The *tympanic membrane* lies in the deepest part of the external auditory meatus and thus forms a lateral or ventral wall of the tympanic cavity, as well as a boundary between the external and middle ear. The membrane is composed of two, more or less distinct portions, the *pars flaccida* (Shrapnell's membrane) and the *pars tensa.* The pars flaccida occupies the tympanic notch; it is separated from the pars tensa by an indistinct band of connective tissue, the *arcus terminalis,* which extends between the anterior and posterior tympanic spines. In many insectivores and bats part of the lateral wall of the epitympanic recess is membranous; distinct limits of the pars flaccida cannot be defined in many of these forms. Microscopically, two or three layers can be distinguished in the pars flaccida. A layer of stratified squamous epithelium, continuous with that of the external auditory meatus, forms an outer layer, the *stratum* cutaneum. An inner layer, the *stratum mucosum,* is continuous with the mucosal lining of the tympanic cavity, and a middle layer, the *substantia propria,* when distinguishable, is composed of loosely organized connective tissue.

The pars tensa fills the area circumscribed by the sulcus tympanicus. Its thin outer and inner layers are continuous with those of the pars flaccida. A middle fibrous layer, the *stratum fibrosum,* is composed of radiating and circular fibers; peripherally, this layer is thickened to form the *annulus fibrosus,* which attaches to the sulcus and/or crista tympanica of the tympanic bone.

The auditory ossicles, *Malleus, incus* and *stapes,* extend across the tympanic cavity and form a system of levers that morphologically and functionally connects the tympanic membrane with the fluids of the inner ear. The *manubrium* of the malleus is embedded

in the tympanic membrane and vibrates with it. Vibrations thus initiated in the malleus are transmitted to the incus through the incudomalleolar articulation; transmission from incus to stapes occurs at the incudostapedial articulation, which incorporates the *lenticular apophysis* (process) of the incus and the articular head of the stapes. These articulations are diarthrodial and are supported by ligamentous articular capsules. The third and terminal articulation, involving the rim (labrum) of the stapedial footplate and the adjacent margins of the fenestra vestibuli, is the *tympanostapedial syndesmosis.* Support, stability, and protection for this chain are provided by the various ligaments of the ossicles, reflections of mucous membrane, and by the intra-aural muscles.

The basic parts of the malleus (Fig. 1) are the *head, neck, mânubrium* and *anterior process.* The head bears an articular surface for the incus; this surface usually exhibits two articular facets. These facets may be distinct and delineated one from another by a groove, or they may merge and give the surface the appearance of a single facet. The *superior* or *lateral facet* is usually the better developed of the two; the other is the *inferior* or *medial articular facet.* The facets are covered by articular cartilage and, at the periphery of each facet, is an *articular* or *capsular* groove which marks the site of attachment of the fibers of the articular capsule. The anteroinferior border of the head is sometimes sharply outlined by a crest, the *capitular crest;* occurring independently, or as an extension of this crest, there may be a prominent anteromedially-directed *capitular spine.*

Arising from the lateral surface of the head near its anterior border, is the neck of the malleus, which generally assumes a rather sigmoid shape. It curves posteriorly and medially, then ultimately downward to merge with the manubrial base. Just before merging with the manubrial base the neck is crossed by the chorda tympani nerve, which notches its inner surface. The *muscular process* for the insertion of the tensor tympani muscle is usually just above this notch. *Manubrial base* is applied to the area of confluence of neck, manubrium, lateral process, orbicular apophysis and the lower part of the anterior process.

The orbicular apophysis is a bony projection which extends posteriorly from the manubrial base; it may be large and massive, or small and scarcely recognizable. The chorda tympani nerve may course across its medial surface and the posterior malleolar fold may attach to it. Projecting into the tympanic membrane from the

manubrial base is the *lateral process* (processus lateralis, brevis). This process is usually small and indistinguishable in gross specimens, but is seemingly consistent in occurrence and is always capped by, or composed entirely of, cartilage.

The manubrium of the malleus is usually saber-shaped and bimarginate. Its tip occupies the deepest part of the concavity of the tympanic membrane (umbo) and is spatulated. This broadening or spatulation may extend along the *membrane margin* of the process as far proximally as the lateral process. The inner, *tympanic margin*, generally forms a rodlike longitudinal support for the manubrium. The membrane margin lies against, and is attached to, the fibrous stratum of the tympanic membrane. The inner surfaces of the manubrium are enveloped by mucous membrane so that the entire process is enclosed between the stratum fibrosum and the stratum mucosum.

The anterior process of the malleus is a composite structure consisting of a *lamina*, *tympanic plate*, and other, less consistent, parts, The lamina is a thin triangular or quadrangular osseous plate which extends anteriorly from the head, neck and manubrial base, to the tympanic plate. Associated with it are a number of variably-developed structures which are well marked in some forms and completely absent in others.

The inferior free margin of the lamina often shows a thickening which extends from the manubrial base toward, or to, the tympanic plate. This is the *pars processus anterioris;* on its inner surface is a longitudinal groove which marks the position of the chorda tympani nerve as it courses across the malleus. In some forms, the central portion of the lamina tends to be thickened; this thickening is called the *central buttress.* Extending anteriorly from the lamina is a thin plate of bone, which lies against, and is attached to, the sulcus malleolaris of the tympanic bone; this is termed the *tympanic plate.* Extending toward the head of the malleus and appearing as a proximal continuation of the tympanic plate are two lamellae, an inner and an outer. The *outer lamella* generally lies in approximately the same plane as the lamina, while the *inner lamella* meets the outer lamella or the lamina at an acute angle. The longitudinal groove or sulcus formed by this union is called the *interlamellar sulcus* or, when it is deep and well marked, *cavum laminae.* The outer lamella is invariably joined to the head; this attachment may be weak and appear as a laminar attachment, or it may be well marked and extensive, in which case the term *pars*

cephalica processus anterioris may be applied. The inner lamella may merge with the head, and it often shows a foramen for the chorda tympani nerve.

The incus (Fig. 1) consists of *body, short process, long process,* and *lenticular process.* The body of the incus provides articular surfaces which articulate with corresponding surfaces of the malleus.

Projecting posteriorly from the body of the incus is the short process (processus brevis), which projects into the fossa incudis and is attached to its posterior wall by the posterior incudal ligament. The long process (stapedial process) projects toward the fenestra vestibuli and parallels the neck of the malleus, with which it articulates by a syndesmosis in some forms. The long process often is grooved or hollowed out so that a *sulcus incudis* is formed. At its distal tip is the lenticular process (Sylvian apophysis), a small cartilaginous disk mounted on an osseous *pedicle.*

The stapes (Fig. 1) consists of *head, anterior* and *posterior crura,* and *footplate.* The head of the stapes, primarily an articular surface, blends with the merged anterior and posterior crura. Near their union with the head, the crura are, in some forms, distinctly expanded; when present, such an expansion is termed the *shoulder* (of the anterior or posterior crus). On the posterior crus, or shoulder, there is a small *muscular process* (processus muscularis stapedius) for the insertion of the stapedius muscle. At their opposite extremities, the crura merge with the footplate, and by so doing form an aperture, the intercrural foramen (obturator foramen) through which the stapedial artery passes in most forms. The surfaces of the crura facing into this aperture are the *intercrural surfaces.* Where these surfaces meet the tympanic surface of the footplate, a crest, which may appear as a continuation of the crura, frequently extends along the long axis of the footplate. This is the *crista stapedis.* Two arches are formed by the crura, one in the area of the head, the *capitular* (inferior) *arch,* and the other at the union of the crura with the footplate, the *basilar* (superior) *arch.* The footplate itself exhibits two surfaces, one facing into the fenestra vestibuli, the *vestibular surface,* and the other facing the tympanic cavity, the tympanic surface. The periphery of the footplate is thickened for the attachment of the annular ligament of the stapes; the peripheral thickening is the *stapedial labrum* and its union to the margins of the fenestra vestibuli by means of the annular ligament forms the *tympanostapedial syndesmosis.*

In addition to capsular ligaments and the annular ligament, the ossicular chain is anchored or supported by the *posterior incudal* and

lateral malleolar ligaments, and by the *suspensory* (superior) *ligaments* of the malleus and incus. Additionally, the tympanic plate of the anterior process is anchored firmly to the tympanic bone by strong fibrous tissue, or by an osseous ankylosis. The lateral malleolar ligament arises from the anterior leg of tympanic bone and attaches to the malleus at the junction of the neck with the head. This ligament may be strong and distinct or may be indistinct and appear only as a mucosal fold. The posterior incudal ligament arises from the roof of the fossa incudis and attaches to the tip of the short process of the incus. The suspensory ligaments of the malleus and incus, frequently absent, are represented by thickened mucosal folds which attach to the head of the malleus and body of the incus, respectively.

The intra-aural muscles, *tensor tympani* and *stapedius*, also support and act upon the ossicular chain. The tensor tympani muscle takes origin from the sphenoid bone, extensions of the cartilage of the Eustachian tube and, occasionally, from the pyriform membrane. It lies along the dorsomedial wall of the tympanic cavity covered by a dense layer of mucous membrane and extends posteriorly in the fossa tensor tympani to approximately the level of the fossula fenestra vestibuli; along this course or at the fossula it bends slightly laterally and attaches to the muscular process on the inner surface of the neck of the malleus. The muscle is innervated by a branch of the trigeminal nerve.

The stapedius muscle lies in a shallow fossa adjacent to the facial nerve, completely outside, but directed toward, the tympanic cavity. As it reaches the mucous membrane of the tympanic cavity, the muscle becomes tendinous and extends to attach to the muscular process of the stapes; in some forms, muscle fibers and the central tendon insert into a small bony or cartilaginous element, the *skeletal element of Paauw*, and from this, the tendon extends toward the muscular process of the stapes. The tendon of insertion often splits into two parts; one inserts directly into the muscular process, the other inserts into the joint capsule and, indirectly, into the lenticular process of the incus. The muscle is innervated by a branch of the facial nerve.

STRUCTURES OF THE MIDDLE EAR IN INSECTIVORA

The middle ear of representative insectivores is generally "primitive" in the mammalian sense of the word. The different families of the order, however, show many structural variations; the major differences seem to be associated with the varied environment and

habits of the specific forms. Descriptions of structures of the middle ear are found in the works of Doran (1878); Bondy (1907), Wilkie (1925; 1929), Cooper (1928), Van der Klaauw (1929; 1931), Stroganov (1945) and in other papers dealing with the cranial morphology and developmental anatomy of specific forms.

FAMILY ERINACIDAE

Erinaceus europaeus

Tympanic Membrane: The tympanic membrane of *Erinaceus* is oval, has a long diameter of approximately 6.2 mm., a short diameter of 4.2 mm., and an area of approximately 20.5 sq. mm. It, with the tympanic bone, is inclined approximately 23 degrees from the horizontal. The membrane shows two more or less distinct parts, the pars flaccida and the pars tensa. The pars tensa occupies the area circumscribed by the sulcus tympanicus; laterally it is essentially delineated from the flaccid portion by a line drawn from the tip of the anterior leg of the tympanic bone to the tip of the posterior leg. The tense portion is concave, with its deepest portion, the umbo, corresponding to the position of the tip of the manubrium. The cutaneous layer is thin but easily recognized in section. The fibrous layer is thick and well developed; peripherally it forms the annulus fibrosus, which is attached to the sulcus tympanicus and the crest of the crista tympanica. The fibrous layer shows thickenings adjacent to the manubrium and in the area where it blends with the substantia propria of the pars flaccida. The stratum mucosum covers the inner surface of the membrane, except in those areas where it is reflected over the manubrium, where it reflects over the anterior process to form the anterior malleolar fold, and over the orbicular apophysis, where it forms the posterior malleolar fold. The thickness of the tense portion is approximately 0.07 mm.

The flaccid portion, occupying the rather large tympanic notch, is thickened peripherally. Its internal surface is covered by mucous membrane, and the external surface by a layer of stratified squamous epithelium continuous with that of the external auditory meatus. The substantia propria is well developed peripherally, but thin centrally where it approaches the pars tensa. Anteriorly this connective tissue attaches to the crest on the inner surface of the postglenoid process of the squamosal, and to the tip of the anterior leg of the tympanic bone. Here it supports the flaccid part of the membrane and helps anchor the anterior leg. In addi-

tion it forms part of the connective tissue of the roof of the external auditory meatus; laterally this tissue blends with the membranous lateral wall of the tympanic cavity and the connective tissue of the meatus. Here it is attached to the mastoid process of the petrosal and its adjacent hyoid process. The flaccid portion varies in thickness from 0.4 mm. to 0.7 mm. at its periphery, to 0.1 mm. where it blends with the pars tensa. Its area is approximately 3.6 sq. mm.

The auditory ossicles of representative Erinacidae have been described by Doran (1878); and more recently by Wassif (1948). These works are, for the most part, comparative and of taxonomic character. My findings agree in all major points with Doran's description of the ossicles of *Erinaceus;* here, however, the ossicles are considered in greater detail since analysis of their function is attempted.

Malleus: The malleus of *Erinaceus* (Fig. 2) has a volume of 1.114 cu. mm. and consists of a head, neck, manubrium, anterior process, and orbicular apophysis. The head of the malleus is small and is best developed in the area of the superior articular facet. The two articular facets merge smoothly at an angle of 140 degrees so that there is no definite limit to either, and the entire articular area has the form of a wide saddle; its periphery is circumscribed by a slight, but distinct capsular groove. Although Doran (1878) indicates the presence of two convex facets, it was probably general appearance to which he was referring. The specimens included in this study showed slightly irregular facets, exhibiting varying degrees of concavity and convexity which varied from specimen to specimen.

The neck of the malleus arises from the base of the inferior articular facet and forms a narrow, cylindrical, slightly-arched process that joins the base of the manubrium distally. The lamina merges with the anterior aspect of the internal border of the neck along its whole length; when viewed from the internal aspect, its form as a cylindrical arch is masked, not only by the lamina, but also by a well-developed muscular process. Between this muscular process and the manubrial base is a notch which marks the point where the chorda tympani nerve crosses the neck.

The anterior process consists of tympanic plate, lamina, inner and outer lamellae, and pars processus anterioris. The pars processus anterioris is best developed near the manubrial base; beyond this point it appears as a slight marginal thickening of the inferior

free border of the lamina and, as it approaches the tympanic plate, it becomes indistinct. Along the junction of the lamina and pars processus anterioris, a well-marked groove indicates the position of the chorda tympani nerve as it courses along the inner surface of the malleus toward its foramen on the inner surface of the inner lamella.

The tympanic process is a prominent flattened projection which lies in the sulcus malleolaris and is attached there by strong bands of fibrous connective tissue. It arises from an area close to the base of the superior articular facet as the inner and outer lamellae, and is supported beneath by the lamina. Proximally, between the two lamellae there is an interlamellar sulcus; in addition, there is a general concavity of the external surface of the tympanic plate except at its tip, which is curved to match the contour of the malleolar sulcus of the tympanic bone. Within this concavity, a shallow groove for the chorda tympani nerve extends distally from the foramen for the chorda tympani nerve; the nerve and a small artery occupy this groove.

The lamina is triangular in shape and has the appearance of a thin osseous plate, filling the area bordered above by the head, posteriorly by the neck and manubrial base, anteriorly by the lamellae and tympanic process, and inferiorly by the pars processus anterioris. These borders support the lamina, and the lamina, in turn, unites all these structures in a single functional unit.

The manubrium is a slender, flattened, bimarginate, osseus process that resembles the blade of a saber when viewed from the side. The length of the manubrium, from tip to lateral process, is 3.0 mm. It is thickened along each of its margins; the tympanic margin is rounded and rodlike; the membrane margin is flattened and has sharp borders to either side. The tip of the manubrium is sharply pointed, only slightly spatulated, and is curved toward the tympanic membrane. Proximally, the manubrium merges smoothly with the manubrial base; here, its membrane surface is modified to form a rounded heel-like protuberance, the lateral process, which is capped by cartilage. Extending posteriorly from this area, and from the manubrial base is a moderately developed orbicular apophysis.

Incus: The incus of *Erinaceus* (Fig. 2) has a total volume of approximately 0.333 cu. mm., and consists of a body, short process, long process and lenticular process. The body of the incus, like the head of the malleus, has a saddle-shaped articular area, and is cir-

cumscribed by a capsular groove. The articular surface has concavities and convexities which are adapted to the corresponding malleolar surfaces. The attachment of the joint capsule is well marked, and forms a rough groove that limits the boundary of the articular surface peripherally, except in the vicinity of the long process; here it extends approximately halfway down the surface of the process; this extension marks the area of attachment of the syndesmosis between malleus and incus. Near the distal extremity of the long process, a short thick pedicle arises from the flattened internal surface of the process; distally the pedicle blends with the thick, discoidal lenticular process. The long process has a length of approximately 0.75 mm.

The short process of the incus, a stout, abruptly tapered projection, has a length of 0.58 mm. It has a slightly lateral curvature, but is directed primarily toward the roof of the tympanic cavity. Its tip is cartilaginous and is usually broken away from ossicles which have been removed.

Stapes: The stapes of *Erinaceus* (Fig. 2) has a volume of 0.172 cu. mm., is roughly stirrup-shaped, and consists of a head, neck, two diverging crura, and an oval footplate. The head of the stapes is low and rounded; it projects from the shoulder, and is approximately aligned with the long axis of the posterior crus. Basally, it is limited by the neck, which is actually a poorly-defined capsular groove. It has a long axis of 0.27 mm. and a short axis of 0.20 mm.

The anterior and posterior crura diverge from the shoulder area to reach their maximum spread approximately midway between the head and the footplate. Terminally, they unite with the footplate to complete the intercrural foramen. Their intercrural surfaces blend to form one continuous surface, smooth and free from any irregularities. Crural sulci are not shown in any of my specimens; this is not in agreement with the observations of Doran (1878). The anterior crus has a length of approximately 1.60 mm., and the posterior a length of 1.55 mm. The outer surfaces of the crura are not as smooth as the inner, either in texture or in contour. Rather than forming a continuous arc, they show slight irregular bends; the posterior exhibits one, while the anterior has two, which are considerable more prominent. The posterior crus is straighter and more massive than the anterior. Near the head it is expanded and flattened to form the posterior shoulder. Two processes project to either side of this; one is the muscular process. The other is unnamed. Doran (1878) states that the muscular process arises from

the posterior part of the head; this apparent discrepancy may be due to a difference in the interpretation of the extent of the head, or perhaps to individual variation. The anterior crus is delicate, strongly arched, and is expanded and flattened near the head to form the anterior shoulder, from which arise two projections that closely resemble those on the posterior crus. Neither of these projections is named, nor appears to have any specific function, other than support. It may be, however, that they have developed in association with the stapedial artery which appears to have some contact with their inner surfaces.

The footplate of the stapes is roughly oval, as is the vestibular window into which it fits; its long axis measures 1.10 mm., its short axis 0.50 mm., and the tympanic surface has an area of 0.40 sq. mm. Its structure and contour are apparently related to the size of the crura, since that part receiving the more massive posterior crus is thick, wide, and shows a distinct convexity on the vestibular surface. Anteriorly, in relation to the anterior crus, the footplate is distinctly thinner and narrower, and the vestibular surface of the footplate shows a flat or slightly concave area. On the tympanic surface of the footplate the two crura sweep inward to merge, not only with the footplate but (weakly) with one another. Thus, the central region of the tympanic surface is raised longitudinally to form a crista stapedis.

Articulations and Attachments: The manubrium of the malleus is bound to the tympanic membrane and lies between its stratum mucosum and stratum fibrosum. The deep layers of the fibrous stratum are attached to the sharp borders of the membrane surface of the manubrium and the stratum mucosum is reflected over these borders to envelop the process.

The incudomalleolar articulation is formed by the saddle-shaped articular surfaces of the malleus and incus. Serial sections show that these two surfaces are covered with articular cartilage, and that the joint is surrounded by an articular capsule, the incudomalleolar capsular ligament. For the most part, the joint, with its capsule and articular cavity, exhibits typical diarthrodial characteristics. At the junction of the two malleolar facets, however, there are areas where the articular cartilages appear to merge and obliterate the joint cavity. Laterally, within the joint cavity, at the periphery of the junction of the superior and inferior articular facets and attached to the inner surface of the articular capsule, there is a small wedge-shaped intra-articular cartilage (meniscus) that partially

subdivides the cavity; this is, however, of small magnitude. There is, in addition, between the neck of the malleus and the long process of the incus, a syndesmosis which extends from the capsular ligament to approximately midway down the long process of the incus.

The lenticular process of the incus articulates with the head of the stapes to form the incudostapedial articulation. The lenticular process consists of a cartilaginous disc mounted on a short, stout, bony pedicle; its flat or slightly convex surface articulates with the cartilage-covered head of the stapes. The joint is supported by a delicate articular capsule, the incudostapedial capsular ligament, which surrounds the joint and attaches to the neck of the stapes and to the pedicle of the lenticular process. Although the articular capsule and a faint line suggesting a separation of the two surfaces are perceptible, an articular cavity, as such, could not be distinguished in serial sections. It may be that the two contiguous surfaces merge, but it is also possible that the articular cavity is obscured in sections studied.

The tympanostapedial syndesmosis consists of strong connective tissue and elastic fibers that connect the cartilaginous labrum of the footplate with the margins of the fenestra vestibuli. This tissue composes the annular ligament of the stapes. Anterosuperiorly the ligament shows a length of 0.055 mm. and a thickness of 0.075 mm. Posteriorly the ligament is approximately 0.20 mm. thick, and its fibers are 0.03 mm. long.

The ossicles, in addition to being bound to one another by capsular ligaments, are fixed to the skeletal elements of the tympanic region. These attachments are quite variable morphologically, and may take the form of strong ligamentous or weak mucosal attachments. The tympanic plate of the malleus is bound by short, strong, dense connective tissue fibers to the sulcus malleolaris of the anterior leg of the tympanic bone. Longer, but equally dense fibers attach both the tympanic plate and the anterior leg of the tympanic bone to the tympanic wing of the alisphenoid and the adjacent crest of the entoglenoid process of the squamosal. The distal tip of the tympanic plate is attached to the medial part of the arterial notch of the alisphenoid wing; this is the most discrete part of the connective tissue in the area and may possibly represent the anterior malleolar ligament of some mammals. Near the tip of the anterior leg, close to the head of the malleus, the connective tissue which joins the tympanic plate and tympanic bone to the

skull is diffuse, and defines a small saccular recess of the middle ear. This connective tissue associated with the anterior leg extends to the crest of bone on the inner surface of the postglenoid process and forms part of the roof of the external auditory meatus and, in the tympanic notch, it contributes further to the meatal roof and, extensively, to the flaccid part of the tympanic membrane. Extensions of this connective tissue to the malleus seem comparable to the lateral malleolar ligament of human anatomy. Extensions of connective tissue related to the proximal borders of the lamellae of the anterior process of the malleus appear to be little more than mucosal folds extending from the shallow epitympanic recess to the head of the malleus and body of the incus. In association with the malleolar head, the connective tissue is slightly thickened to form suspensory supports; that to the malleolar head is the superior or suspensory ligament of the malleus, and its continuation onto the body of the incus is the superior incudal ligament. Mucosal reflections continue from this to extend from the incudal fossa to the short process of the incus where they constitute the incudal fold.

The incus has a firm attachment to the roof of the tympanic cavity where its short process extends into a rather deep fossa incudis and is enveloped by strong connective tissue fibers which radiate from the walls of the fossa to the cartilaginous tip of the short process. Additional anchorage is accomplished by a synchondrosis between the cartilaginous tip and the wall of the fossa. These connections constitute the posterior incudal ligament (Fig. 32).

The stapes is held in place by its annular ligament and by its ligamentous attachment to the lenticular process of the incus. In addition, it, like the other ossicles, is weakly supported by a reflection of the mucous membrane, the stapedial fold. The stapedial artery is also enveloped by mucous membrane as it passes through the intercrural foramen. This artery, with its connective tissue, is closely associated with, and appears to be bound to, the inner surface of the intercrural foramen; its strongest connection is with the intercrural surface of the shoulder of the anterior crus.

Intra-aural Muscles: The tensor tympani muscle is well developed; anteriorly, at its origin it is thick and wide, while posteriorly it tapers to a short cylindrical tendon. Its structure does not appear to be pennate, but rather of a thick parallel type. The muscle has a diameter of approximately 0.7 mm. and a length of 2.75-3.0 mm. Its position on the labyrinthine wall is well marked by the fossa tensor tympani, which lies posterior to the alisphenoid-

petrosal suture, medial to the stapedial artery, lateral to the artery of the promontory, and anterior to most of the promontory. The muscle fibers originate from the dense, thick connective tissue covering the adjacent bone, especially that part associated with the alisphenoidpetrosal suture and the anterior carotid foramen. The muscle is strongly enveloped by connective tissue and is covered on its external surface by the mucous membrane of the tympanic cavity. Near the fossula fenestrae vestibuli the muscle arches laterally and inserts on the muscular process of the malleus by a single cylindrical tendon. The muscle has a total volume of 0.764 cu. mm., of which 0.744 cu. mm., is muscle and 0.020 cu. mm., is tendon.

The stapedius muscle is slender, flattened and penniform. It has a length of approximately 2.3 mm. and a volume of 0.490 cu. mm. The muscle has its origin from the medial and posterior walls of the foramen stylomastodeum primitivum. Its position in this foramen is marked by a shallow fossa which is separated from the groove transmitting the facial nerve. The belly of the muscle is embedded in the connective tissue that fills the foramen; only its tendon is covered with the mucous membrane of the tympanic cavity. The muscle inserts on the muscular process of the stapes by a short cylindrical tendon; this tendon is not ossified, does not show a skeletal element of Paauw, and does not send a slip to the incudostapedial articular capsule, as it does in many mammals.

Family Soricidae

Cryptotis parva

Tympanic Membrane: The tympanic membrane of *Cryptotis* is oval, inclined (with the tympanic bone) approximately 23 degrees from the horizontal, and it consists of two parts, the pars tensa and the pars flaccida. The membrane measures approximately 1.9 mm. along its long axis, and 1.3 mm. along the shorter axis; its area is approximately 1.9 sq. mm. The thickness varies from 0.003 mm. to 0.0012 mm., the thicker portions occupying the area adjacent to the manubrium of the malleus.

The pars tensa consists of the usual three layers, stratum cutaneum, stratum fibrosum and stratum mucosum. This part of the membrane is attached to the sulcus tympanicus by the fibers of the annulus fibrosus, which is merely the thickened perimeter of the stratum fibrosum. In some parts of this annulus one or two vascular channels may be seen, but these are not comparable in size, structure or appearance to the cavernous tissue associated with

the annulus of Chiroptera. Superiorly (actually laterally, this case) the fibers of the annulus attach to the border of the anterior leg of the tympanic bone; neither a sulcus nor a crista tympanica is present in this area.

The pars flaccida occupies the tympanic notch; its boundaries are not clearly demarcated since the lateral wall of the epitympanic recess and the roof of the external auditory meatus blend in this area. The flaccid portion consists of typical stratum cutaneum and stratum mucosum, which are slightly thicker than the same layers on the pars tensa. The substantia propria is scanty.

Malleus: The malleus of *Cryptotis* (Fig. 5) has a volume of 0.034 cu. mm.; it differs from that of the other insectivores considered in the presence of a prominent capitular crest, and a central laminar crest. When viewed under magnification the malleus appears to be composed of two major masses, an upper and a lower, connected by a thin, delicate, semitransparent lamina; the upper mass is represented by the head, the lower by the massive orbicular apophysis.

The head of the malleus is rounded both anteriorly and superiorly; anteroinferiorly it is wedge-shaped and sharply outlined by the capitular crest; inferiorly it is flat, even though the lamina and lamellae merge with it. The malleolar head has a height of 0.32 mm., a length of 0.45 mm., and a breadth of 0.35 mm. The articular surface consists of superior and inferior articular facets. The superior facet has a height of 0.20 mm., faces posteriorly, is concave, and is separated from the inferior by a shallow groove. The inferior facet has a length of 0.20 mm., is small (less than half the size of the superior), convex, and is elongated posteriorly. The two facets meet at an angle of approximately 110 degrees.

The anterior process consists of a tympanic plate, inner and outer lamellae, and a lamina with its laminar crest. Except in size, the tympanic plate and lamellae closely resemble those of *Erinaceus*. The tympanic plate is long, concave on its anterior surface, and is attached to the tympanic bone by a fibrous ankylosis. The inner and outer lamellae represent the proximal part of the plate; both merge with the inferior border of the head below the capitular crest. The inner lamella is perforated by the chorda tympani nerve; between the two lamellae is an interlamellar sulcus. The lamina is quadrangular in shape, shows a central bend on its external surface and, on its inner surface, a sharp crest extends from the mus-

cular process on the neck to the middle of the lamina. A pars processus anterioris and central buttress are absent.

The neck of the malleus arises from the lateral side of the head. It is broad and well-marked at its origin, but tapers posteriorly until it reaches the posterior border of the inferior articular facet, beyond which it appears as a thickened border of the lamina; it maintains this character as it bends 90 degrees to approach the manubrial base. Near this base, on its inner surface, is a well-developed muscular process for the insertion of the tensor tympani muscle.

An extremely large orbicular apophysis forms the most massive part of the ossicle. In line with the long axis of the manubrium, on the membrane surface of the manubrial base is a small cartilaginous lateral process. The manubrium of the malleus is saber-shaped, similar to that of *Erinaceus*, except that it is not recurved at its tip; it has a length of 0.9 mm. and, except along its tympanic margin, is composed of bone.

Incus: The incus of *Cryptotis* (Fig. 7) is small, has a volume of approximately 0.013 cu. mm., and is characterized by a relatively massive body, a roughly cylindrical long process and a poorly developed (essentially absent) short process. There are four, more or less distinguishable articular areas on the body of the incus. These four areas are formed by subdivisions of the superior and inferior articular facets; the inferior facet thus shows medial and lateral areas which articulate with the inferior articular facet of the malleus, and the superior facet is divided into medial and lateral areas which articulate with the superior facet of the malleus. The lateral areas of the incus are supported by the main mass of the body, while the medial areas occupy the ventral surface of a ledge-like projection. On the superior surface of the body is a small cartilaginous tubercle which represents the short process. This process is probably broken off of most isolated ossicles and is, therefore, not seen on the gross specimen.

The long process of the incus is roughly cylindrical; it narrows distally and is rounded at its tip. The process has a slight dorsal curvature and is approximately 0.42 mm. long. The lenticular process is an oval cartilaginous disc; it lies at the end of a slightly curved, flattened pedicle and shows long and short diameters of 0.12 and 0.07 mm., respectively.

Stapes: The stapes of *Cryptotis* (Fig. 6) is characterized by strongly divergent crura which, with the footplate, form a circular

intercrural foramen through which the stapedial artery passes. The head of the stapes is a flattened plate covered by articular cartilage. The articular surface is oval and measures 0.018 mm. and 0.096 mm. in its short and long diameters. A sharply pointed, posteriorly directed, muscular process lies at the junction of the head and posterior crus.

The posterior crus is slightly longer than the anterior and shows a crural sulcus in the area of the capitular arch. This sulcus takes a spiral course as it sweeps from the undersurface of the head toward the stapedial base. The stapedial sulcus occupies only the cephalic half of the intercrural surface. The anterior crus is more cylindrical; its intercrural surface is flattened and does not show a crural sulcus. At the base of the footplate the two crura converge and unite with the tympanic surface of the footplate, where a well-marked crista stapedis extends along the long axis of the footplate. The footplate has a long diameter of 0.24 mm. and a short diameter of 0.16 mm.; its area is 0.03 sq. mm. The anterior crus of the stapes has a length of 0.35 mm., the posterior crus a length of 0.32 mm. and the stapes has a total volume of 0.003 cu. mm.

Attachments and Articulations: The manubrium of the malleus is embedded and firmly anchored in the tympanic membrane by fibers of the stratum fibrosum. This stratum and, also, the fibers of the arcus terminalis, appear to have strong connections with the lateral process. The orbicular apophysis is not in contact with the membrane, but, extending between it and the inner surface of the membrane is the posterior incudal fold. Anteriorly, a similar fold is reflected from the tympanic membrane over the lamina to form the anterior malleolar fold. Superiorly, the mucous membrane is reflected from the roof of the tympanic cavity to the head of the malleus and the body of the incus. It is slightly thickened over the area of the incudomalleolar articulation to form the suspensory ligaments of the malleus and incus. Another, rather thick, mucosal fold extends from the roof of the tympanic cavity and adjacent tensor tympani muscle to the crest on the inner surface of the lamina; the relationship between this fold and the tensor tympani muscle may explain the development of this crest.

The attachment of the tympanic plate to the tympanic bone is accomplished mainly by a fibrous ankylosis; the tip and the distal parts of the medial and lateral borders of the tympanic plate show small areas where an osseous ankylosis is present. This, however, is not extensive, and it only vaguely resembles that seen in Chiroptera. A lateral malleolar ligament is wanting.

The posterior incudal ligament is a single fibrous connection extending from the posterosuperior wall of the fossa incudis to the cartilaginous tubercle which represents the short process of the incus. The form of the posterior incudal ligament in *Cryptotis* is simple when compared with the double ligamentous structures possessed by other forms included in this investigation. The incudomalleolar and the incudostapedial articulations are both typically diarthrodial in that they possess cartilage covered articular surfaces and distinct articular capsules.

The fibers of the annular ligament of the stapes connect the cartilaginous labrum of the footplate with the cartilaginous margins of the fenestra vestibuli to form the tympanostapedial syndesmosis. The length of the fibers of the annular ligament does not appear to vary significantly around the perimeter of the footplate; the thickness of the ligament, however, is slightly greater posteriorly than anteriorly. The length of the fibers of the ligament is approximately 0.025 mm. throughout its circumference, while the thickness varies from 0.016 mm. anteriorly to 0.025 mm. posteriorly. The annular ligament and the stapedial footplate are covered on their external surfaces by the mucous membrane of the tympanic cavity, and by the internal periosteum on the surfaces facing toward the vestibular periotic cistern.

Intra-aural Muscles: The tensor tympani muscle of *Cryptotis* is very small; it arises from the ventral surface of the connective tissue covering the pyriform fenestra and extends posterolaterally along the ventral surface of this connective tissue. As the muscle approaches the anterior border of the fossula fenestrae vestibuli it becomes tendinous and bends sharply over a trochlea formed by a band of dense fibrous connective tissue. The lateral part of this trochlear band attaches to the thin bony roof of the tympanic cavity just medial to the artery of the promontory; the medial part of the band attaches to the cochlear wall beneath the stapedial artery. This relationship of the tensor tympani to the trochlea is not present in any of the other forms utilized in this investigation; it resembles the condition found in man, where the tensor tympani bends around the cochleariform process. The muscle inserts by a single cylindrical tendon into the muscular process of the inner surface of the neck of the malleus. The muscle and its tendon are covered by the mucous membrane of the tympanic cavity. The tensor tympani is innervated by a branch from the trigeminal nerve, and measurements indicate that the muscle has a total volume of

approximately 0.02 cu. mm. Of this volume 0.007 cu. mm. is tendon and 0.016 cu. mm. is muscle.

The stapedius muscle of *Cryptotis* is a small, triangular, multipennate muscle, which lies beneath the jugulohyoid in a small depression posterior to the basal turn of the cochlea. The muscle courses anteromedially beneath the facial nerve; its tendon enters the tympanic cavity through a small fissure between the tympanohyal and the petrosal bone and inserts on the muscular process of the stapes. A skeletal element of Paauw is not present. The muscle has a length of 0.77 mm. and a total volume of 0.07 cu. mm. The motor innervation of the stapedius is by a branch of the facial nerve. In addition, a rather large branch of the glossopharyngeal nerve enters the substance of the muscle where it breaks up into two or three smaller branches. It could not be determined whether these fibers form a proprioceptive sensory supply to the muscle, or, rather, pass through it into the tympanic cavity to contribute to the tympanic plexus.

FAMILY TALPIDAE

Scalopus aquaticus

Tympanic Membrane: The tympanic membrane of *Scalopus* roughly resembles a quadrangle with rounded corners. Its surface is irregular with concave and convex areas associated with those parts of the malleus which lie deep to the membrane. The membrane is flattened where the neck of the malleus, anterior process and manubrial base lie against it; it is sharply convex where the lateral process projects into it, and deeply concave at the umbo.

The membrane has a total area of approximately 11.3 sq. mm.; its long and short axes show lengths of 4.0 and 3.5 mm., which correspond to the same diametric measurements cited by Gaughran (1954). The membrane varies in thickness from 0.013 mm. peripherally, to 0.035 mm. centrally, where the fibers of the fibrous stratum are thickened in the area of the manubrium. The annulus fibrosus anchors the membrane peripherally and is attached mainly to the crista tympanica; basally (laterally), some of the fibers are inserted into a shallow sulcus tympanicus. Since the tympanic bone is fused almost indistinguishably with the surrounding bones of the skull, the tympanic notch and its associated pars flaccida are indistinct. The pars flaccida, however, can be distinguished in sections, and is characterized by the absence of a middle layer (substantia propria), and by the discreteness of the mucous and cutaneous strata. The attachment between the malleus and the

membrane is peculiar in *Scalopus* in that the fibrous stratum has an extensive attachment to the anterior process in addition to its typical attachment to the manubrium and lateral process.

Malleus: The malleus of *Scalopus* (Fig. 8) has been superficially described by Gaughran (1954), and has been figured by Stroganov (1945). Although it is basically like that of *Erinaceus* and *Cryptotis*, its parts and processes are greatly modified.

The malleus has a total volume of 0.300 cu. mm.; the head is relatively large, having a height of 1.0 mm., a width of 0.68 mm. and a length of 1.25 mm. Its articular surface for the incus appears as a narrow, slightly bent oval. A slight concavity occurs in the area of the superior (lateral) facet, and a slight convexity is present in the area of the inferior (medial) facet. The recognition of facets, however, is purely arbitrary since the surface is essentially flat. The neck of the malleus is a relatively long (1.25 mm.) thick column of bone, oval in cross-section. The lamina merges with the entire length of its anterior border; distally the neck bends anteroinferiorly to join the manubrial base.

The anterior process consists of a small tympanic plate, a lamina and inner and outer lamellae; the tympanic plate occupies the extreme tip of the anterior process and is attached strongly to a rudimentary sulcus malleolaris. The inner lamella parallels the outer lamella and is joined to it by a thin connecting plate so that together, the two lamellae appear U-shaped in cross-section; thus, a deep sulcus, or cavum laminae is formed. The outer lamella forms the upper border of the lamina and thickens as it merges with the head of the malleus to form a cephalic process. The exact meaning of the term "cephalic process" as it is used by others is a confusing issue in the literature. Gaughran (1954) states that he found no suggestion of a processus cephalicus in *Scalopus*, but Stroganov (1954), concerning the auditory ossicles of the North American Scalopinae, says that a short, stout processus cephalicus arises from the external side of the head. This apparent discrepancy is probably the result of different interpretations of a "cephalic process" as opposed to an outer lamella, or a massive upper border of the lamina which unites with the head. My own observations indicate that, in these forms, the cephalic process is merely a massive union of the outer lamella, or lamina, to the anterior part of the head. The lamina is a thin triangular sheet of bone that merges with the head, and with the neck as far distally as the manubrial base.

The manubrial base is small and is represented by the distal bend of the neck; it is smooth and rounded, but does not bulge or show a definite orbicular apophysis. The manubrium of the malleus projects anterosuperiorly; the lateral process projects anteromedially into the tympanic membrane. The manubrium is a thin osseous plate which is bimarginate; it has a flat membrane surface with sharp borders to either side. Its length, from tip to lateral process, is approximately 1.75 mm.

Incus: The incus of *Scalopus* (Fig. 9) has a relatively large body with a flattened articular surface. It has a volume of approximately 0.22 cu. mm.; arising from it are the long and short processes.

The articular surface faces anteriorly, has a length of 1.25 mm., and a breadth of 0.687 mm. Near the center of the articular area there is a slight valley that more or less separates the surface into two parts, an inferior (medial) area which articulates with the inferior articular facet of the malleus and which is slightly convex, and a superior (lateral) area which is slightly concave and articulates with the inferior facet of the malleus.

The short process is a conical, posteriorly-directed projection. It has a length of approximately 0.5 mm., is sharply pointed, and has a depression on its ventral surface, at the depths of which lies a small nutrient foramen. The long process is thin and straight, and has a prominent sulcus incudis on its anterior surface; at its tip is a circular depression which faces posteromedially, and from which arises the pedicle of the lenticular process. The long process has a length of approximately 1.4 mm. The lenticular process is oval, entirely cartilaginous, and has a length of 0.38 mm. along its long axis, and 0.20 mm. along its shorter axis.

Stapes: The stapes of *Scalopus* (Fig. 10) has a volume of 0.044 cu. mm.; it is stirrup-shaped and is characterized by strongly divergent crura and a flat, thin footplate. The head of the stapes is an oval disc, which is conspicuously wider than the crural shoulders on which it lies. Its articular surface is slightly convex and is larger than the corresponding surface of the lenticular process, with which it articulates. Its long axis has a length of approximately 0.4 mm. and the short axis has a length of 0.2 mm.

The anterior crus is considerable more arched than the posterior. Its cephalic half is cylindrical and is thicker than the basal half; the latter is flattened from side to side, and its base is somewhat triangular. The posterior crus is shorter, wider and straighter than the anterior. Near its capitular end is a globular prominence with

a short posteriorly-directed spine, which represents the muscular process. The basal ends of both crura are sharply bordered. The anterior crus is approximately 1.2 mm. long, the posterior approximately 0.9 mm.

The footplate of the stapes is an elongate oval, widest posteriorly and narrowest anteriorly. The tympanic surface is concave and shows a peripheral thickening, while the vestibular surface is convex, more strongly posteriorly than anteriorly. The crura merge with the tympanic surface of the footplate at right angles to its surface, and their sharp intercrural surfaces extend along the long axis of the surface to form a low crista stapedis. The footplate has a length along its long axis of approximately 1.9 mm.; the width of the footplate varies from 0.72 mm. posteriorly, to 0.48 mm. anteriorly.

Attachments and Articulations: The manubrium of the malleus is embedded in the tympanic membrane between the stratum fibrosum and stratum mucosum. The inner fibers of the fibrous stratum attach to the membrane borders of the manubrium, and all of the fibers of this stratum, in the area of the manubrial base, appear to attach to the lateral process. Anteriorly the fibrous stratum appears to have extensive attachments to the free border of the anterior process. The neck, lamina and the remainder of the external surface of the anterior process are also in contact with the fibrous stratum, but do not appear to have definite connections with it.

The tympanic plate of the malleus is anchored by fibrous connective tissue and, to a lesser extent, by a cartilaginous and osseous ankylosis. The plate lies in a shallow sulcus malleolaris and is attached both to the sulcus and to the adjacent squamosal. Additional anchorage of the tympanic plate is provided by a flat fibrous band that arises from the lateral wall of the Glaserian fissure. On the dorsal surface of the plate, surrounding the chorda tympani nerve, is a mass of loosely-organized connective tissue which fills the fissure and extends into the tympanic cavity as a small vertical band, which extends from the roof of the cavity to the chorda tympani nerve and tympanic plate. In the European mole, *Talpa*, Wilkie (1929) has recognized an anterior malleolar ligament, which he describes as a band of connective tissue passing through the Glaserian fissure, receiving supporting fibers from a flat fibrous band, and passing backward and downward along a deep groove in the inner laminar wall of the malleus. This description fits that of the course of the chorda tympani nerve in *Scalopus*, and it ap-

pears likely that he has mistaken this structure for a ligament in gross examination. This discrepancy has also been suggested by Gaughran (1954). In its anterior course, from its entrance into the tympanic cavity to the manubrial base, the chorda tympani nerve lies in contact with the pars flaccida of the tympanic membrane. The relationship of this nerve to the pars flaccida, and the relationship of the anterior process and neck of the malleus to the tympanic membrane, do not allow for the development of mucosal folds; thus, neither an anterior malleolar fold nor a posterior is developed in *Scalopus*.

The head of the malleus and the body and short process of the incus are suspended from the roof of the tympanic cavity by thickened mucosal folds which form the superior or suspensory ligaments of the malleus and incus. Beyond the limits of the incudomalleolar articulation the mucosal folds continue onto the short process of the incus where they constitute the incudal fold.

In the sections studied in this investigation, a discrete lateral malleolar ligament could not be identified; there was, however, extending from the tympanic bone to a point near the junction of the head and neck of the malleus, a weak mucosal fold which corresponds closely in position to the lateral malleolar ligament of other forms.

The posterior incudal ligament is double; one firm strong band arises from the posterior and medial wall of the fossa incudis and passes forward and slightly downward to attach to the cartilaginous tip of the short process. A more lateral band, considerably denser and seemingly stronger, passes medially and slightly backward to attach to the lateral side of the tip of the short process. These two parts of the posterior incudal ligament are entirely separate. Wilkie (1929) states that the processus brevis (short process) of the European mole (*Talpa*) attaches to the wall of the recess by an articulation; he describes the wall of the recess and the tip of the process as being covered by hyaline cartilage, and the joint as being surrounded by a capsular ligament. This arrangement is not present in any of the specimens of *Scalopus* examined. The posterior incudal ligament of *Scalopus* closely resembles that of the Chiroptera, described below.

The incudomalleolar articulation is peculiar in that the articular surfaces of the malleus and incus are essentially flat and are not separable into superior and inferior facets. In the articulated position the malleolar articular surface faces posteriorly and the in-

cudal anteriorly. Each surface is covered by articular cartilage and exhibits typical diarthrodial characteristics. The incudostapedial articulation is also typically diarthrodial; its articular capsule is supported and reinforced posteriorly by a distinct slip of the tendon of the stapedius muscle.

The annular ligament of the tympanostapedial syndesmosis is longest and thinnest around the anterior curvature of the footplate. Anteriorly the fibers of the ligament have a length of 0.042 mm. and the ligament is approximately 0.014 mm. thick. Around the posterior curvature of the footplate the fibers have a length of 0.027 mm. and the ligament is 0.015 mm. thick. The thickness is, thus, fairly uniform throughout.

Intra-aural Muscles: The tensor tympani is wanting in *Scalopus.* The stapedius muscle is small, poorly developed, and penniform. It is directed anteromedially and dorsally toward the tympanic cavity, and lies entirely within a bony canal of its own. This canal is situated near the anteromedial border of the stylomastoid foramen, and is closed externally by a layer of connective tissue; the majority of the muscle fibers take origin from this connective tissue and extend the length of the canal. Some fibers arise from the bony walls of the canal; these are shorter, fewer in number and give the muscle its penniform appearance. The muscle is largest at its base where it has a diameter of approximately 0.16 mm. The muscle has a total length of approximately 1.12 mm. and a volume of 0.033 cu. mm. The tendon of the muscle is cylindrical, covered by mucous membrane, and it inserts into the muscular process of the stapes and sends a slip to the incudostapedial articular capsule.

STRUCTURES OF THE MIDDLE EAR IN CHIROPTERA

Equivalent parts of the middle ear among various species of Microchiroptera show a basic similarity in structure; variations may be encountered in the degree of inclination of the tympanic membrane, in the size, shape and mode of attachment of the intra-aural muscles, in the parts and processes of the ossicles, and the detailed morphology of the posterior incudal ligament. Descriptions of the ossicles in some representative bats are found in the works of Doran (1878) and Wassif (1948). The form of the tensor tympani in a number of bats has been described by Wassif (1950).

FAMILY PHYLLOSTOMATIDAE

Glossophaga soricina

Tympanic Membrane: The tympanic membrane of *Glossophaga* is oval, and has a long diameter of 2.0 mm. and a short diameter of 1.6 mm.; the thickness of the membrane varies from 0.002 mm. peripherally, to approximately 0.0064 mm. centrally, where the fibrous stratum is thickened adjacent to the manubrium of the malleus.

The pars tensa consists of an outer stratum cutaneum, a middle stratum fibrosum and an inner stratum mucosum. The stratum cutaneum is very thin and is best distinguished in sections where it is thickened around the manubrium, or where it is modified peripherally to form the annulus fibrosus. The fibers comprising the annulus fibrosus insert into the sulcus tympanicus; superiorly, the sulcus is absent and the membrane attaches to the ventral surfaces of the anterior and posterior legs of the tympanic bone. In the latter areas the annulus is thin and is not spread out into a fan-shaped attachment as it is in the wide basal portion of the sulcus tympanicus. Where the sulcus is present on the tympanic bone, the fibers of the annulus intermingle with an extensive network of blood vessels which form the cavernous tissue; this tissue is not present superiorly. Since the tips of the two tympanic legs are joined by a cartilaginous ankylosis, neither a tympanic notch nor a distinct pars flaccida is distinguishable. The pars flaccida, however, is represented superiorly where the cutaneous and mucous strata are thickened, and the annulus fibrosus and stratum fibrosum are replaced by the substantia propria.

Malleus: The malleus of *Glossophaga* (Fig. 11) has a volume of 0.027 cu. mm.; its head exhibits a sharply-pointed capitular spine projecting toward the tympanic plate. The head is approximately 0.27 mm. high, 0.42 mm. long, and 0.30 mm. wide. The superior and inferior articular facets subtend an angle of approximately 95 degrees. The superior facet is considerably larger than the inferior; it has a height of 0.18 mm., and a breadth of 0.32 mm. The inferior articular facet tapers posteriorly, has a breadth (anteriorly) of approximately 0.22 mm., and a length of 0.15 mm.

The anterior process is composed of tympanic plate, lamina, inner and outer lamellae, central buttress, and pars processus anterioris. The tympanic plate extends onto the tympanic bone, with which it is indistinguishably fused by an osseous ankylosis, to the sulcus

malleolaris. The proximal portion of the tympanic plate is represented by the inner and outer lamellae, which are supported below by the lamina. The inner lamella is a thin bony plate which arises as an inner perpendicular shelf of the lamina; it is broadest distally, narrowest proximally, and is pierced from below by the chorda tympani nerve. The outer lamella appears as a thickened, rod-like upper margin of the lamina. The outer lamella merges with the anterior part of the base of the head, along with, and continuous with, the laminar attachment to the head. The inner lamella usually does not attach to the head; it may, however, show a connective tissue union with it. A shallow, almost indistinguishable interlamellar sulcus is present between the two lamellae. The lamina is quadrangular and exhibits two thickenings, a central buttress and a pars processus anterioris. The rather thick central buttress arises from the area of the muscular process and extends forward, almost as far as the undersurface of the inner lamella; it is thick posteriorly and thin anteriorly. Arising from the area of the manubrial base is a short, relatively massive pars processus anterioris; its apex lies in the central portion of the lamina rather than along its inferior margin as it does in most other forms. On the inner surface of the lamina, between the central buttress and the pars processus anterioris, is the groove for the chorda tympani nerve. The remainder of the lamina is thin, semitransparent, and is reinforced by connective tissue.

The neck of the malleus arises from the anterolateral aspect of the head, sweeps posteriorly and medially as a lateral bony shelf of the head and lamina, bends downward, and continues into the manubrial base. At its origin, on the anterolateral side of the head, is a small tubercle for the attachment of the lateral malleolar ligament. On its medial side, just below the point where it bends downward, is the upper part of the muscular process. This process is a crest of bone that extends inferiorly to the lower border of the manubrial base. Extending posteriorly from the manubrial base is a rounded, well-developed orbicular apophysis.

The manubrium of the malleus extends anteroinferiorly and inward. It is saber-shaped, bimarginate, and composed almost entirely of cartilage; it is spatulated at its tip, and its membrane margin is broadened along its entire length. It has a length of 1.12 mm. from tip to lateral process. The lateral process appears as a heel-like projection of the manubrial base and extends into the tympanic membrane.

Incus: The incus of *Glossophaga* (Fig. 13) has a volume of approximately 0.016 cu. mm., and consists of a body, short process, long process and lenticular process. The body is rather small and supports the cartilaginous articular surface, which articulates with the malleus and is a mirror image of that surface. The short process is stout, approximately 0.21 mm. long, and has a rounded tip. The long process is highly irregular and shows a thick inner border and a relatively thin outer border. Along the dorsal surface of the long process is a vascular groove which leads into a minute nutrient foramen at the angle between the long and short process; this angle is approximately 88 degrees. The anterior surface of the long process (facing toward the neck of the malleus) does not show a distinct sulcus incudis, but does show a shallow irregular channel which results from the differences in thickness between the medial and lateral margins of the process. Projecting medially from the rounded tip of the process is a delicate, slightly flattened pedicle of the lenticular process. The lenticular process is disc-like, entirely cartilaginous, and has a long diameter of 0.13 mm. and a short diameter of 0.10 mm. The length of the long process is approximately 0.32 mm.

Stapes: The stapes of *Glossophaga* (Fig. 12) is a delicate structure characterized by prominent crural sulci which give the entire ossicle a "hollowed-out" appearance. The stapes and its intercrural foramen are triangular in shape; the ossicle has a volume of approximately 0.0036 cu. mm.

The head of the stapes is a flattened oval disc covered by articular cartilage, and demarcated from the rest of the ossicle by a distinct capsular groove which circumscribes its base. The long axis of the articular surface of the head measures approximately 0.140 mm., and the shorter axis approximately 0.105 mm. The two crura are continuous beneath the head, and their prominent crural sulci form a deep excavation in the undersurface of the head. On the head, at the junction of the head and posterior crus, is a sharply pointed muscular process for the tendon of the stapedius muscle. The posterior crus is more massive than the anterior, but is almost identical in form. Both crura show prominent crural sulci along the entire lengths of their intercrural surfaces; basally, the margins of the crura tend to follow the peripheral margins of the footplate. The anterior crus has a length of 0.35 mm. and is straighter than the posterior crus; the posterior crus is approximately 0.28 mm. long.

The footplate of the stapes is roughly oval, the posterior curvature

being greater than the anterior. The stapedial labrum is thickest posteriorly, thinnest anteriorly, and is composed entirely of cartilage. Centrally the footplate is composed of very thin (0.004 mm.) bone which is supported by fibrous connective tissue. In some areas, especially anteriorly, this fibrous tissue completely replaces the bone. Posteriorly, beneath the base of the posterior crus, the vestibular surface of the footplate is convex; anteriorly this surface is essentially flat. On the tympanic surface of the footplate the posterior portion is concave and the anterior essentially flat. The long and short axes of the footplate measure 0.42 mm. and 0.25 mm., respectively; the area of the vestibular surface is approximately 0.075 mm.

Attachments and Articulations: The manubrium of the malleus lies between the stratum fibrosum and the stratum mucosum of the tympanic membrane. The fibers of the fibrous stratum attach to the broadened margins of the membrane surface of the manubrium; these fibers also anchor the lateral process into the membrane. Neither an anterior nor a posterior malleolar fold is present.

The union of the tympanic plate to the sulcus malleolaris is by means of a fibrous ankylosis proximally and an osseous ankylosis distally. The lateral malleolar ligament is a strong discrete band of tissue, which arises from the anteromedial side of the anterior leg of the tympanic bone; it extends posteriorly and attaches to a small tubercle on the anterolateral side of the head of the malleus.

The posterior incudal ligament is composed of a strong band of ligamentous tissue, which extends from the lateral wall of the fossa incudis to the lateral surface of the tip of the short process. Extending from the medial wall of the fossa to the medial surface of the tip of the short process is a thickened mucosal fold. This fold and the lateral ligamentous band give the ligament a bipartite character. A small saccular recess lies above the tip of the short process; this is bounded medially and laterally by the two components of the ligament, inferiorly by the tip of the short process, and superiorly by the roof of the fossa incudis, which is covered by a relatively dense layer of connective tissue; within this tissue is a small cartilage which appears to be sesamoid in character. The posterior surface of the tip of the short process is supported by weak extensions from the tissue which occupies the roof.

The incudomalleolar articulation is formed by the deeply-cut, cartilaginous articular surfaces on the head of the malleus and the body of the incus. The joint is surrounded by an articular capsule

and it exhibits typical diarthrodial characteristics. Because of the deeply-cut, congruent articular surfaces, the joint is capable of being tightly locked. An extension of the joint capsule onto the long process of the incus adds a small degree of stability to the articulation.

The incudostapedial articulation involves the cartilaginous lenticular process of the incus and the cartilage-covered articular head of the stapes. The articular surface of the stapedial head is slightly larger than that of the lenticular process and allows a small amount of gliding and rolling to take place. These movements are limited by the incudostapedial capsular ligament, which completely envelopes the joint and appears to be supported posteriorly by extensions of the fibers of the tendon of the stapedius muscle. The fibers of the capsular ligament insert into the groove circumscribing the head of the stapes, and into the periostium around the pedicle of the lenticular process.

The annular ligament of the stapes extends from the cartilaginous walls of the fenestra vestibuli to the cartilaginous stapedial labrum; the ligament and these structures constitute the tympanostapedial syndesmosis. The fibers of the annular ligament are longest anterosuperiorly (0.009 mm.) and shortest posteroinferiorly (0.0035 mm.) The thickness of the ligament varies from 0.035 mm. anteriorly, to 0.062 mm. posteriorly.

Intra-aural Muscles: The tensor tympani is a flattened muscle arising from the pyriform membrane, the dorsal and ventral surfaces of an extension of the cartilage of the Eustachian tube, and from the anterior part of the petrosal bone. The muscle lies in a shallow fossa on the petrosal bone; as it approaches the level of the fossula fenestrae vestibuli it bends slightly laterally, becomes tendinous, and inserts into the muscular crest (process) on the inner surface of the malleus. The tensor tympani has a total volume of approximately 0.090 cu. mm., of which 0.048 cu. mm. is muscle, and 0.042 cu. mm. is tendon.

The stapedius muscle is a small, triangular, multipennate muscle arising from the medial, superior and lateral walls of the small bony fossa, which lies between bulges formed by the lateral semicircular canal and the basal whorl of the cochlea. The muscle narrows to a thin cylindrical tendon which passes beneath the facial nerve; the tendon is embedded in adipose tissue and contains a small cartilaginous skeletal element of Paauw, which lies just beneath the mucous lining of the tympanic cavity. Extending from this

element to the muscular process of the stapes is a thin tendinous strand enveloped by mucous membrane. The stapedius muscle has a total volume of approximately 0.047 cu. mm.

Family Rhinolophidae

Rhinolophus ferrum-equinum

Tympanic Membrane: The tympanic membrane of *Rhinolophus* is nearly circular in outline; it has a long diameter of 2.0 mm., a short diameter of 1.7 mm., an area of approximately 2.5 sq. mm. and it is inclined approximately 82 degrees from the horizontal. It varies in thickness from 0.003 mm. peripherally, to 0.0045 mm. centrally where its fibrous stratum is slightly thickened. Peripherally the middle fibrous layer is expanded to form the annulus fibrosus, which intermingles with the cavernous tissue and attaches into the sulcus tympanicus. Since the anterior and posterior legs of the tympanic bone meet and fuse, one with the other, a tympanic notch is not distinguishable. Here the membrane lacks an annulus fibrosus and contains a scanty substantia propria, which extends between the fused tympanic legs and the upper border of the membrane. This part of the membrane represents the pars flaccida; its boundaries, however, are not distinct.

Malleus: The malleus of *Rhinolophus* has a volume of 0.042 cu. mm.; its head is small and globular, and shows deeply-cut articular facets. The head has a height of 0.60 mm., a length of 0.56 mm. and a breadth of 0.38 mm. The superior articular facet has a convex medial portion and a concave lateral portion, and it appears to be almost twice as large as the inferior facet; it has a height of 0.23 mm. and a breadth of 0.38 mm. The superior facet faces posteriorly and the inferior facet dorsally, so the two facets subtend an angle of approximately 90 degrees. The inferior facet has a length of 0.21 mm. and a breadth of 0.24 mm. across its widest part. The facet tapers posteriorly and is conspicuously narrower than the superior facet.

The neck of the malleus arises from the anterolateral aspect of the head, sweeps posteriorly and medially as a lateral bony shelf on the head and lamina, bends downward, and continues into the manubrial base. At its origin, on the anterolateral side of the head, is a small tubercle for the attachment of the lateral malleolar ligament. On the internal surface of the neck is a prominent muscular crest, which extends from the point where the neck bends downward to

the level of the manubrial base; just below it is the notch formed by the chorda tympani nerve. The tensor tympani muscle inserts by a single cylindrical tendon into the upper edge of the crest, rather than along its entire border.

The anterior process consists of tympanic plate, lamina, inner and outer lamellae, central buttress and pars processus anterioris. The tympanic plate lies in the sulcus malleolaris of the tympanic bone and is merged with it by an osseous ankylosis. Its proximal portion is represented by the inner and outer lamellae, which are supported below by the lamina. The outer lamella is thicker than the inner and lies in a different plane so that a well-marked sulcus laminae lies between the two lamellae. The outer lamella merges with the head, while the inner does not. The inner lamella is thin, flattened and plate-like, and is pierced by the chorda tympanic nerve. The central portion of the lamina is thickened by a central buttress, which traverses the greater part of the lamina, extending from the area of the muscular process forward to the level of the upper margin of the lamina. The remainder of the lamina is thin and semitransparent, except for its inferior free border which is slightly thickened by a rather indistinct pars processus anterioris. Between the pars processus anterioris and the central buttress is the groove for the chorda tympani nerve.

Because of a well-developed orbicular apophysis, the manubrial base appears massive. On the membrane surface of the manubrial base is a small cartilaginous lateral process, which lies at the proximal end of the axis of the manubrium. The manubrium is a slightly curved, bimarginate, saber-shaped process which has a length of 1.31 mm. from tip to lateral process. Its membrane surface is slightly spatulated at the tip of the process, and is slightly broadened along most of its length. The manubrium is entirely cartilaginous, except for the slightly thickened tympanic margin, which is osseous.

Incus: The incus of *Rhinolophus* has a small body, the major mass of which is a cartilage-covered articular surface for the malleus. The short process arises from the anterior part of the body and extends posterosuperiorly. The process has a length of 0.21 mm. and shows a slight curvature. In serial sections through the incus, the tip of the short process appears to be bifid, showing medial and lateral portions which provide areas for the attachment of the medial and lateral components of the posterior incudal

ligament. The long process is roughly cylindrical; it tapers toward its distal extremity, shows a shallow sulcus incudis, and has a length of 0.38 mm. Projecting medially from the tip of the long process is a short, cylindrical pedicle for the lenticular process. The lenticular process itself is a roughly circular, cartilaginous disc which has a diameter of 0.10 mm. The entire ossicle has a total volume of approximately 0.013 cu. mm.

Stapes: Based on the study of serial sections through the middle ear, the stapes of *Rhinolophus* appears to have the following features. The head is rounded, covered by a thin layer of articular cartilage, and has a diameter of approximately 0.115 mm. The anterior and posterior crura are slightly divergent and form, with the footplate, the boundaries of a triangular intercrural foramen, which transmits the stapedial artery. Both crura are more or less cylindrical in the area of the capitular arch; basally, however, they show crural sulci; the posterior crus is slightly more massive than the anterior and shows a deeper crural sulcus. Both crura unite with the cartilaginous labrum of the footplate and tend to follow its contour at each pole. The anterior crus is slightly longer than the posterior, measuring approximately 0.60 mm., as compared to 0.45 mm. for the posterior. Based on measurement of the fenestra vestibuli the footplate has long and short diameters of 0.56 mm. and 0.35 mm., respectively. Stretching across the basal part of the labrum of the footplate is the membranous central portion, which appears to be composed mostly of elastic fibers. The footplate of the stapes has an area of approximately 0.15 sq. mm., and the entire stapes has a total volume of approximately 0.0038 cu. mm.

Attachments and Articulations: The manubrium of the malleus lies in the tympanic membrane between the stratum mucosum and the stratum fibrosum; it is anchored by the fibrous stratum, which attaches strongly to the spatulated edge of the manubrium and the lateral process and weakly to the remainder of the membrane margin of the manubrium. The presence of mucosal folds in the middle ear could not be determined because of tissue disruptions resulting from poor fixation. There are, however, suggestions of suspensory folds for the malleus and incus; anterior and posterior malleolar folds also appear to be present.

A small, but discrete, lateral malleolar ligament arises from a small spine of the inner surface of the anterior leg of the tympanic bone; the ligament parallels the outer lamella of the anterior process

and attaches to a small tubercle on the anterolateral surface of the head of the malleus.

The posterior incudal ligament consists of two separate ligamentous bands; one arises from the medial wall of the fossa incudis and passes to the medial part of the bifid tip of the short process. The other band arises from the lateral wall of the fossa and attaches to the lateral portion of the bifid tip. The posterior part of the tip of the short process is also anchored weakly by a mucosal reflection, which is supported by varying amounts of connective tissue.

Both the incudomalleolar and the incudostapedial joints are typically diarthrodial; their articular surfaces are covered by cartilage, and the joints are supported by articular capsules. The deeply-cut articular surfaces of the malleus and incus permit close coupling and locking. The slight difference in size between the surfaces of the lenticular process and the head of the stapes permits limited movement at the incudostapedial articulation.

The fibers composing the annular ligament of the stapes are longest anteriorly where they measure approximately 0.0143 mm. The length of these fibers gradually decreases toward the posterior pole of the footplate where their average length is approximately 0.0074 mm. The annular ligament is thickest posteriorly and thinnest anteriorly, measuring 0.074 mm. at the posterior curvature of the footplate, and 0.0185 mm. at the anterior curvature.

Intra-aural Muscles: The tensor tympani is a small spindle-shaped muscle, which inserts by a single cylindrical tendon into the end of a somewhat crest-like muscular process. The muscle fibers arise mainly from the dorsal surface of the posterior extension of the cartilage of the Eustachian tube; the muscle lies along the anterolateral wall of the bony cochlea within a canal of slightly thickened mucous membrane. It has a volume of 0.280 cu. mm., of which 0.162 cu. mm. is muscle and 0.118 cu. mm. is tendon.

The stapedius muscle is typically multipennate; the fibers arise from the fossa stapedius and insert into the central tendon of the muscle and into the cartilaginous skeletal element of Paauw. Extending from this element to the muscular process of the stapes is a small cylindrical tendon. The stapedius muscle has a total volume of 0.05 cu. mm., and is innervated by a branch of the facial nerve.

Family Natalidae

Natalus mexicanus

Tympanic Membrane: The tympanic membrane of *Natalus* is oval; it has a long diameter of 1.36 mm., a short diameter of 1.10 mm., an area of approximately 1.2 sq. mm., and is inclined approximately 60 degrees from the horizontal. The microscopic structure of the membrane follows the basic pattern in that it is composed of an outer stratum cutaneum, an inner stratum mucosum and a middle stratum fibrosum; the latter is modified peripherally to form the annulus fibrosus, and is thickened centrally where the fibers insert into the cartilaginous edges of the manubrium and the minute lateral process. The pars tensa averages approximately 0.004 mm. in thickness, except centrally where the thickened fibrous layer increases the thickness to 0.008 mm. The fibers of the annulus insert into the sulcus tympanicus, intermingled with the cavernous tissue.

The pars flaccida is ill-defined, of small magnitude and occupies the tympanic notch. This part of the membrane is thicker than the pars tensa, owing to an increase in the thickness of its inner and outer layers. The middle layer is composed of loosely organized connective tissue, which blends superiorly with the connective tissue of the external auditory meatus. Mucosal folds are essentially absent; the only one present appears to be the posterior malleolar fold, which extends from the pars flaccida to the orbicular apophysis and to the posterior tympanic wall in association with the cartilaginous "caudal Chordafortsatz" of Bondy.

Malleus: The malleus of *Natalus* (Fig. 14) has a volume of 0.028 cu. mm. Its head is small and globular, except superiorly where the articular facets are deeply cut. The head has a height of 0.20 mm., a length of 0.50 mm., and a breadth of 0.20 mm. The superior articular facet faces posteriorly and the inferior dorsally, so the two facets subtend an angle of approximately 90 degrees. The superior facet is considerably larger than the inferior and shows a roughly circular outline, in contrast to the elongate triangular outline exhibited by the inferior facet. The superior facet has a height of 0.13 mm. and the inferior a length of 0.15 mm.

The neck of the malleus arises from the anterolateral side of the head, extends posteriorly and medially as a lateral bony shelf on the head and lamina, bends downward and becomes lost in a relatively large bony mass associated with the muscular process for the tensor tympani muscle. Its distal extent can arbitrarily be defined

as the notch or groove for the chorda tympani nerve. At its origin, on the anterolateral side of the head is a small tubercle for the attachment of the lateral malleolar ligament. The muscular process is a prominent, sharply pointed spine on the inner surface of the neck.

The anterior process consists of tympanic plate, lamina, inner and outer lamellae, and central buttress. The tympanic plate lies in the sulcus malleolaris of the tympanic bone and is merged indistinguishably with it by an osseous ankylosis. The inner and outer lamellae, which represent its proximal continuation, are peculiar in that the inner is thick and massive and the outer is thin and delicate; this form is somewhat opposite to that in other bats, where the outer lamella is usually the thickest and the inner lamella is thin and plate-like. A well-marked interlamellar sulcus occupies the area between the two lamellae. The lamina is roughly quadrangular and is supported by a rather massive central buttress, which extends from the area of the muscular process forward for approximately two-thirds of the anteroposterior length of the lamina. Because of the central buttress the internal surface has an irregular bent appearance; the external surface is smooth and free from any irregularities. Anteriorly, both surfaces of the lamina are reinforced by fibrous connective tissue.

Projecting posteriorly from the manubrial base is a small, but distinct, orbicular apophysis. The manubrium of the malleus is extremely thin and delicate; it is bimarginate, saber-shaped, sharply pointed and composed entirely of cartilage. The manubrium has a length, from tip to short process, of 0.85 mm. Its distal third shows a slight spatulation. At the base of the manubrium is a small cartilaginous lateral process, which projects into the tympanic membrane.

Incus: The incus of *Natalus* (Fig. 16) has a volume of approximately 0.007 cu. mm. The body is small and its processes are relatively stout and well developed. The short process arises from the anterior part of the body, projects posterosuperiorly, and has a length of 0.18 mm. Its tip is bluntly rounded and is capped by cartilage. The angle formed between the long and short process is rather acute (55 degrees) in comparison with that of other bats studied, where the angle tends to be approximately 90 degrees. The long process is flattened dorsoventrally and shows a sulcus incudis on its ventral surface; this sulcus is shallow distally but deep proximally in the area of the articular surface, which appears to

extend into its proximal part. Bending medially from the tip of the long process is a slightly flattened osseous pedicle, on the tip of which is a disc-like lenticular process. The long process has long and short diameters of 0.10 mm. and 0.07 mm., respectively.

Stapes: The stapes of *Natalus* (Fig. 15) has a triangular intercrural foramen, a prominent muscular process, prominent crural sulci, a partially membranous footplate, and a volume of approximately 0.007 cu. mm. The head is small, flattened, slightly concave and is covered by articular cartilage. Extending posteriorly from the head is a sharply pointed muscular process, which appears to incorporate part of the articular surface. Circumscribing the head and extending onto the muscular process is a capsular groove for the incudostapedial capsular ligament. Both crura have well-developed crural sulci, which excavate their entire intercrural surface and the undersurface of the head. The posterior crus is slightly more massive than the anterior and is slightly straighter. Both crura join the cartilaginous labrum of the footplate and follow its curvatures at each end; the footplate of the stapes is circumscribed by the cartilaginous labrum. The central portion of the footplate has the appearance of a tightly-stretched membrane which occupies the area circumscribed by the labrum. This portion is mostly fibrous but shows some bone posteriorly. The footplate shows long and short diameters of 0.38 mm. and 0.25 mm., respectively, and its area is approximately 0.047 sq. mm.

Attachments and Articulations: The manubrium of the malleus lies between the stratum mucosum and stratum fibrosum; the inner fibers of the fibrous stratum attach strongly to the margins along the membrane border of the manubrium, particularly to its spatulated portion. Superiorly, the fibers are strongly attached to the lateral process.

The tympanic plate is firmly fixed to the tympanic bone by an osseous ankylosis, and by a fibrous ankylosis to the proximal part of the sulcus malleolaris. The dorsal surface of the tympanic plate is completely devoid of fibrous connections; along this surface lies the chorda tympani nerve; surrounding this nerve, and separating the plate from the squamosal bone above, is a pad of adipose tissue.

The lateral malleolar ligament arises from the anterior leg of the tympanic bone as a distinct, roughly cylindrical ligament; it parallels the outer lamella of the anterior process and inserts into a minute tubercle on the anterolateral side of the head, close to the origin of the neck.

The posterior incudal ligament consists of a strong ligamentous lateral component, which extends from the lateral wall of the fossa incudis to the lateral side of the tip of the short process, and a medial fibrous component, which arises from the medial cartilaginous wall of the fossa and attaches to the medial side of the cartilaginous tip of the short process. Posteriorly, the tip of the process is weakly connected to the fossa by fibrous tissue. A small saccular recess occupies the space enclosed by the components of the ligament and limited above by the roof of the fossa.

Suspensory folds of the malleus and incus are weakly developed in some areas and lacking in others. They are best developed between the roof of the tympanic cavity and the head and body of the incus, and to a lesser extent along the short process of the incus (incudal fold). In none of these areas are the folds thickened to form true suspensory ligaments.

The incudomalleolar articulation involves the cartilaginous articular surfaces on the head of the malleus and body of the incus. The joint is surrounded by an articular capsule and it exhibits typical diarthrodial characteristics. Because of the deeply cut, congruent articular surfaces, the joint is capable of being tightly locked.

The incudostapedial articulation involves the cartilaginous lenticular proces of the incus and the cartilage-covered head of the stapes. The articular surface of the stapedial head is slightly larger than that of the lenticular process and allows a small amount of movement to take place. Movements at this point are limited by the incudostapedial articular capsule, which completely envelops the joint; because of the close association of the musclar process with the articular surface of the stapes, it is probable that the capsule is reinforced posteriorly by the tendon of the stapedius muscle.

The structures which constitute the tympanostapedial syndesmosis are the cartilaginous walls of the fenestra vestibuli, the stapedial labrum and the annular ligament, which extends between and unites these parts. The fibers of the annular ligament are longest anterosuperiorly and shortest posteriorly; they measure 0.11 mm. and 0.0065 mm., respectively. The ligament is thinnest anteriorly and thickest posteriorly, measuring 0.020 mm. and 0.043 mm., respectively.

Intra-aural Muscles: The tensor tympani is a small spindle-shaped muscle with a sharply pointed tendon. The muscle arises from the sphenoid bone and, more extensively, from extensions of

the cartilage of the auditory tube. The muscle courses laterally and posteriorly, becomes tendinous and inserts by a single pointed tendon onto the muscular process of the malleus. The muscle is innervated by a special branch of the mandibular division of the trigeminal nerve; this branch passes through the otic ganglion and along the inner border of the styliform process of the tympanic bone to gain access to the dorsal border of the cartilage of the auditory tube and the muscle itself. The muscle has a volume of 0.095 cu. mm., of which 0.068 cu. mm. is muscle, and 0.027 cu. mm. is tendon.

The stapedius muscle is small and multipennate; its tendon occupies the central axis of the muscle and appears to be ossified throughout most of its length. The muscle has a volume of approximately 0.047 cu. mm. and has embedded within its tendon a bony skeletal element of Paauw; this element lies just beneath the mucous lining of the tympanic cavity. Extending from the skeletal element to the muscular process of the stapes is a thin, delicate tendon, which attaches to the muscular process of the stapes and appears to intermingle with the fibers of the posterior part of the articular capsule.

Family Vespertilionidae

Eptesicus fuscus

Tympanic Membrane: The tympanic membrane of *Eptesicus* is oval, has a long diameter of 2.0 mm., a short diameter of 1.75 mm., and an area of approximately 3.0 sq. mm. The membrane is inclined approximately 54 degrees from the horizontal and varies in thickness from 0.0037 mm. peripherally, to 0.0087 mm. centrally. The microscopic structure of the membrane follows the basic pattern; the stratum cutaneum and stratum mucosum are simple epithelial layers, except where they are thickened over the pars flaccida. A middle fibrous stratum is present in the pars tensa, and a scanty substantia propria forms the middle layer of the pars flaccida. The fibrous stratum has a strong attachment to the manubrium of the malleus, especially its spatulated tip, and to the minute lateral process. The substantia propria blends with the connective tissue of the roof of the external auditory meatus, and with this tissue is attached to the distal ends of the tympanic legs and to the squamosal bone above. This tissue of the pars flaccida anchors the membrane superiorly and is essentially limited to the tympanic notch.

Malleus: The malleus of *Eptesicus* (Fig. 17) has a volume of 0.037 cu. mm. From its medial aspect the head of the malleus has a globular appearance, except for the deeply-cut articular surface.

When viewed from the lateral side, the head shows an anteroposterior elongation owing to the neck, which sweeps around the anterior pole of the head. The superior articular facet faces essentially posteriorly and the inferior superiorly, so the two facets subtend an angle of approximately 90 degrees. The head has a length of 0.37 mm., a height of 0.50 mm. and a breadth of 0.37 mm. The superior articular facet has a height of 0.20 mm. and the inferior a length of 0.20 mm. Both facets are rather similar in shape; the superior is slightly more circular and is slightly larger than the inferior articular facet.

The neck of the malleus arises from the extreme anterolateral surface of the head and sweeps around its lateral surface, where it appears as a lateral shelf of the head. The neck extends past the level of the inferior articular facet and extends posteroinferiorly as a thickening of the posterosuperior part of the lamina. The neck bends downward and is thickened in association with the muscular process on its inner surface. Before joining the manubrial base it is crossed, on its inner surface, by the chorda tympani nerve. The muscular process lies just above the chorda tympani nerve and is represented by a single tubercle.

The anterior process consists of tympanic plate, lamellae, lamina, central buttress, and pars processus anterioris. The tympanic plate lies in the sulcus malleolaris of the tympanic bone and is anchored to it by an osseous ankylosis. The inner and outer lamellae, which appear as proximal continuations of the plate, are delicate structures. The outer lamella is thicker than the inner, is somewhat rodlike, and is joined to the undersurface of the head of the malleus. The inner lamella is thin and platelike and does not join distinctly with the head. The lamellae are supported from below by the lamina, and between them is a shallow interlamellar sulcus. The thin quadrangular lamina is supported by a central buttress and by a pars process anterioris along its inferior border. The central buttress is well developed; it extends from the area of the muscular process forward across the central portion of the lamina. The pars processus anterioris extends forward from the manubrial base along the free border of the lamina; it is distinguishable in the gross specimen for only about half the length of the inferior border. On the medial surface of the lamina, between the pars processus anterioris and the central buttress, is a groove for the chorda tympani nerve. This nerve courses forward in the groove, pierces the inner lamella and then lies along the dorsal surface of the tympanic plate. Except for

the central buttress and the pars processus anterioris, the lamina is essentially fibrous rather than osseous; this, however, appears to vary from specimen to specimen.

The manubrial base is the largest part of the ossicle owing to the size of the orbicular apophysis, which is rather massive, relative to the size of the ossicle. The manubrium of the malleus is saber-shaped, has a thickened tympanic margin, a sharply-pointed tip, and a distinct curvature. It is entirely cartilaginous and shows a slight spatulation of its tip; the membrane margin is not broadened, except for this spatulation. At the proximal end of the manubrium, on the membrane surface of the manubrial base, is a cartilaginous lateral process. The manubrium has a length of 1.12 mm.

Incus: The incus of *Eptesicus* (Fig. 19) has a volume of 0.0143 cu. mm., and, except for its articulating surfaces, it is entirely osseous. The short process is stout and well developed; it projects posterodorsally into the fossa incudis, has a blunt rounded tip, and has a length of 0.21 mm. The long process shows a sulcus incudis on its anterior (anteroinferior) surface; within this sulcus is a distinct arterial groove, which courses toward the body of the incus and terminates in a small nutrient foramen. The long process has a length of 0.56 mm.; its distal end is blunt and slightly flattened, and projecting medially from it is the relatively long, flat, twisted pedicle of the lenticular process. The lenticular process is a cartilaginous disc having long and short diameters of 0.21 mm. and 0.14 mm., respectively.

Stapes: The stapes of *Eptesicus* (Fig. 18) has a small, flattened head bearing the articular surface for the incudomalleolar articulation. Its articular surface is oval, covered by articular cartilage, and has long and short diameters of 0.21 mm. and 0.14 mm., respectively. At the posterior part of the head, at its junction with the posterior crus, is a small muscular process for the tendon of the stapedius muscle. The ossicle has a volume of 0.0051 cu. mm., and is characterized by an extremely delicate anterior crus.

The two crura diverge from the head and, with the footplate, outline a triangular intercrural foramen. The posterior crus is considerable more massive than the anterior, and is straighter, and shorter. The posterior crus has a length of 0.34 mm. and the anterior 0.41 mm. Basally, the crura unite with the stapedial labrum of the footplate. Toward the head, in the area of the capitular arch, the sulci are indistinct and wide so that one margin of the sulcus is prominent while the other is indistinct. Because of this, the margin

of the intercrural surface of the capitular arch is crest-like. The footplate is oval, and is slightly narrower anteriorly than posteriorly. The long diameter measures approximately 0.45 mm. and the short diameter 0.20 mm. Except for the thickened cartilaginous labrum, the footplate is flat and thin; its central portion appears to be entirely membranous. The tympanic surface has an area of 0.063 sq. mm.

Attachments and Articulations: The lateral malleolar ligament is strong and distinct; it arises from a small spine on the anterior leg of the tympanic bone, parallels the outer lamella of the anterior process, and inserts on a small tubercle at the junction between the head and the neck of the malleus.

The tympanic plate is firmly attached to the tympanic bone by an osseous ankylosis distally and a fibrous ankylosis proximally. The upper surface of the tympanic plate is completely devoid of fibrous connections; on this surface, the chorda tympani nerve courses distally surrounded by numerous blood vessels. The nerve and the tympanic plate are separated from the squamosal bone by pads of fat.

The posterior incudal ligament is bipartite and consists of a lateral and a medial component, both of which are strongly developed in all the Vespertilionidae studied. The lateral component extends from the lateral side of the roof of the fossa incudis and attaches to the lateral side of the tip of the short process. The medial component arises from the medial wall and attaches to the medial side of the short process near its tip. Between the tip and the roof of the fossa is a small saccular recess.

The incudomalleolar articulation involves the cartilaginous articular surfaces of the head of the malleus and body of the incus. The joint is surrounded by a delicate articular capsule and exhibits typical diarthrodial characteristics. The deeply-cut articular surfaces of the two ossicles permit close-coupling and locking. The incudostapedial articulation is also typically diarthrodial; the articular surfaces, however, are not of equal size and the small difference in size permits some gliding and rolling movements. This joint appears to be supported by the tendon of the closely-associated stapedius muscle; the incudomalleolar articulation receives reinforcement by an extension of its capsular fibers onto the long process of the incus. The latter, however, is of small extent and probably is a reminant of a stronger syndesmosis between the malleus and incus, such as that described in *Erinaceus* and *Cryptotis*. There are no suspensory folds or ligaments associated with the ossicular chain in *Eptesicus* or in any of the other Vespertilionidae studied.

The annular ligament of the stapes unites the cartilaginous margins of the fenestra vestibuli with the stapedial labrum, and, with these, forms the tympanostapedial syndesmosis. The fibers of the annular ligament are longest anterosuperiorly and shortest posteriorly. Their length varies from 0.010 mm. around the anterior curvature of the footplate, to 0.005 mm. around the posterior curvature. The ligament is thinnest anteriorly and thickest posteriorly, measuring 0.0175 mm. and 0.043 mm., respectively.

Intra-aural Muscles: The tensor tympani is a small spindle-shaped muscle which arises from the posterior extension of the cartilage of the Eustachian tube, the sphenoid bone and, probably, from the pyriform membrane. It inserts by a sharply-pointed tendon into the muscular process on the inner surface of the neck of the malleus. The muscle has a total volume of 0.131 cu. mm., of which 0.123 cu. mm. is muscle and 0.0075 cu. mm. is tendon. It is innervated by the trigeminal nerve via a branch which lies along the dorsal surface of the muscle.

The stapedius muscle is small and is typically multipennate. It arises from the walls of the fossa stapedius and passes toward the tympanic cavity, where it passes under the facial nerve, receives its motor innervation from a small twig of this nerve, and terminates in association with an osseous skeletal element of Paauw, which lies just beneath the mucous membrane of the tympanic cavity. Extending from this element to the musclar process of the stapes is a small, cylindrical tendon. The muscle has a total volume of 0.200 cu. mm.

Myotis velifer

Tympanic Membrane: The tympanic membrane of *Myotis* has a long diameter of 1.9 mm., a short diameter of 1.6 mm., an area of approximately 2.4 sq. mm., and, with the tympanic bone, it is inclined approximately 45 degrees from the horizontal. In all other respects the membrane is essentially identical to that of *Eptesicus*, described above.

Malleus: Except for size, the malleus of *Myotis* (Fig. 20) has the same features as those described for *Eptesicus*. The head has a height of 0.20 mm., a length of 0.37 mm., and a breadth of 0.20 mm. The superior and inferior articular facets subtend an angle of approximately 95 degrees; the superior facet has a height of 0.13 mm. and the inferior facet a length of 0.20 mm. The manubrium of the malleus has a length of 1.04 mm. and the entire ossicle has a volume of approximately 0.046 cu. mm.

Incus: The morphology of the incus of *Myotis* is similar to that described above for *Eptesicus*. The incus of *Myotis* (Fig. 22) has a volume of 0.014 cu. mm.; the long process has a length of 0.38 mm., the short process a length of 0.19 mm. and the two processes subtend an angle of 90 degrees. The lenticular process has a long diameter of 0.14 mm. and a short diameter of 0.12 mm.

Stapes: The stapes of *Myotis* (Fig. 21) also resembles that of *Eptesicus*, but is smaller in volume and shows deeper crural sulci. The long and short diameters of the head are 0.18 mm. and 0.12 mm., respectively. The anterior crus has a length of 0.35 mm. and the posterior crus a length of 0.36 mm. The footplate has a long diameter of 0.40 mm., a short diameter of 0.24 mm. and the area of its vestibular surface is approximately 0.075 sq. mm. The entire ossicle has a volume of 0.0037 cu. mm.

Attachments and Articulations: The annular ligament of the stapes is longest and thinnest anteriorly, and thickest and shortest posteriorly. The fibers vary in length from 0.007 mm., around the anterior curvatures of the footplate, to 0.005 mm. around the posterior curvature. The ligament varies in thickness from 0.035 mm. anteriorly to 0.043 mm. posteriorly. In all other respects, the morphology of the tympanostapedial syndesmosis, the ossicular articulations, and the mucosal folds and ligaments are similar to those described above for *Eptesicus*.

Intra-aural Muscles: The tensor tympani and stapedius muscles in *Myotis* resemble those of the other Vespertilionidae considered in this investigation. The tensor tympani muscle has a total volume of 0.099 cu. mm., of which 0.061 cu. mm. is muscle and 0.038 cu. mm. is tendon. The stapedius muscle has a volume of 0.105 cu. mm.

Plecotus townsendii

The morphology of the tympanic membrane, auditory ossicles, articulations, ligaments, and intra-aural muscles of *Plecotus* is similar to that described for *Eptesicus*. The structures, however, are considerably larger in proportion to the size of the animal.

Tympanic Membrane: The tympanic membrane has a long diameter of 3.10 mm., a short diameter of 2.6 mm. and an area of approximately 6.3 sq. mm. The membrane is inclined approximately 55 degrees from the horizontal, and the pars tensa varies in thickness from 0.0018 mm. peripherally, to 0.0045 mm. centrally.

Malleus: The malleus of *Plecotus* (Fig. 23) is characterized by deeply-cut articular facets which subtend an angle of approxi-

mately 68 degrees. The head of the malleus has a height of 0.55 mm., a length of 0.57 mm., and a breadth of 0.43 mm. The superior articular facet has a height of 0.28 mm. and the inferior facet a length of 0.20 mm. The manubrium of the malleus has a length of 1.63 mm. from tip to lateral process. The malleus has a total volume of approximately 0.092 cu. mm.

Incus: The incus of *Plecotus* (Fig. 25) has a volume of 0.21 cu. mm.; its long process measures 0.63 mm. in length, its short process is 0.18 mm. long, and the two processes subtend an angle of approximately 100 degrees. The lenticular process has a long diameter of 0.15 mm., and a short diameter of 0.13 mm.

Stapes: The stapes of *Plecotus* (Fig. 24) has a volume of 0.0045 cu. mm. The head has a long diameter of 0.18 mm. and a short diameter of 0.15 mm. The length of the anterior crus is 0.49 mm.; the posterior crus is 0.42 mm. in length. The footplate of the stapes has long and short diameters of 0.51 mm. and 0.35 mm., respectively; the vestibular surface has an area of approximately 0.14 sq. mm.

Articulations and Attachments: The fibers of the annular ligament vary in length from 0.013 mm. around the anterior curvature of the footplate, to 0.0087 mm. around the posterior curvature. The ligament has a thickness of 0.035 mm. anteriorly and 0.051 mm. posteriorly.

Intra-aural Muscles: The spindle-shaped tensor tympani has a volume of 0.130 cu. mm., of which 0.10 cu. mm. is muscle and 0.03 cu. mm. is tendon. The stapedius muscle has a total volume of 0.126 cu. mm.

Family Molossidae

Tadarida brasiliensis

Tympanic Membrane: The tympanic membrane of *Tadarida* is large and somewhat rounded, having diameters of 2.8 mm. and 2.3 mm. in its long and short axes. The membrane has a total area of approximately 5.0 sq. mm., varies in thickness from 0.002 mm. peripherally to 0.008 mm. centrally, and it is inclined approximately 50 degrees from the horizontal.

Structurally the tympanic membrane is similar to that of the other bats described above. The pars tensa occupies the area circumscribed by the sulcus tympanicus, while the pars flaccida occupies an ill-defined area between the tips of the two legs of the tympanic bone. The pars tensa is covered externally by the stratum cutaneum, internally by the stratum mucosum, and its middle stratum fibrosum

is extremely thin, except centrally where it is thickened in the area of the umbo, and peripherally, where it is expanded to form the annulus tympanicus. The stratum cutaneum and stratum mucosum are thickened on the surfaces of the pars flaccida; here the substantia propria is scanty, blends peripherally with the connective tissue of the external auditory meatus and anchors the membrane superiorly.

Malleus: The malleus of *Tadarida* (Fig. 26) has a volume of 0.140 cu. mm. and is characterized by a prominent capitular crest and spine; the crest is continuous with the neck of the malleus along the lateral side of the head. This association gives the ossicle a peculiar appearance; it appears as if it were mounted and delicately balanced on a thin crest of bone, represented by the lamina. The head has a height of 0.50 mm., a length of 0.67 mm. and a breadth of 0.42 mm. The articular facets are deeply cut and subtend an angle of approximately 100 degrees. The superior articular facet has a height of 0.26 mm. and a breadth equal to that of the head. The inferior facet is smaller in area than the superior because of its narrowness; it has a length of approximately 0.28 mm.

The neck of the malleus resembles that of other bats, but is extremely thin and delicate. It appears as a continuation of the capitular crest on the lateral side of the head, then extends posteriorly and sweeps medially as a lateral bony shelf of the head and upper border of the lamina. Posteriorly it bends downward and is considerably thickened as it approaches the manubrial base. Extending medially from the inner surface of the neck is a sharp crest which represents the muscular process. At each end of the crest is a small tubercle for the insertion of the two tendons of the tensor tympani muscle.

The anterior process is distinctive in *Tadarida* and in other molossids studied. It consists of tympanic plate, inner and outer lamellae, lamina and pars processus anterioris. The tympanic plate is firmly attached to the sulcus malleolaris of the tympanic bone. The inner and outer lamellae, which represent the plate proximally, are similar, one to the other, in appearance. The lamellae join at an acute angle so that a deep prominent interlamellar sulcus is formed; in cross-section the sulcus is V-shaped. The outer lamella is joined to the head, while the inner lamella ends abruptly, rather than tapering to its termination as it does in most other bats. The lamina is thin, but is supported by a thin central buttress and is reinforced by fibrous connective tissue which covers its inner and outer sur-

faces. Its inferior border is thickened in the area of the manubrial base by a short pars processus anterioris.

The manubrial base appears large because of the massive orbicular apophysis, which extends posteriorly. On the membrane surface of the manubrial base is a small lateral process. The manubrium of the malleus is saber-shaped and bimarginate. It is composed of cartilage, has a length of 1.5 mm., and is slightly spatulated at its tip. The remainder of the membrane surface appears as a sharp edge. The tympanic margin of the manubrium is thickened and is somewhat rodlike.

Incus: The incus of *Tadarida* (Fig. 28) has a volume of 0.027 cu. mm. Its body is small and shows an articular surface which is a mirror image of the malleolar articular surface. The short process is relatively small and blunt, and has a length of 0.18 mm.; the tip of the process is capped by cartilage. The long process of the incus has a length of 0.70 mm., and has a deep sulcus incudis which excavates its entire anterior surface. Projection medially from the tip of the long process is a long cylindrical pedicle, which carries the disc-like lenticular process; the latter has a diameter of 0.12 mm.

Stapes: The stapes of *Tadarida* (Fig. 27) has a volume of 0.007 cu. mm. The head of the stapes is circular; its diameter is approximately 0.14 mm. On the posterior crus, at its junction with the head, is a well-developed, pointed, muscular process. The posterior crus is characterized by a distinct curvature in its basal part. The anterior crus is slightly curved and is less massive than the posterior. The crural sulcus is poorly developed on the intercrural surfaces of both crura, but is slightly more prominent on the anterior crus. Both crura join the cartilaginous stapedial labrum; the margins of each crus follow the curvatures at each end of the footplate. The anterior crus has a length of 0.42 mm., and the posterior crus a length of 0.35 mm. The footplate of the stapes is an irregular oval, much broader posteriorly than anteriorly, and shows a distinct curvature of its vestibular surface. The long diameter of the footplate is 0.56 mm., the short diameter is 0.23 mm., and the area of the vestibular surface is approximately 0.094 sq. mm.

Attachments and Articulations: The manubrium of the malleus is embedded in the tympanic membrane and is anchored by the fibers of the fibrous stratum which are attached distally to the spatulated tip of the manubrium and to its sharp border proximally. The fibrous stratum is, also, firmly attached to the cartilaginous lateral process. The annulus fibrosus attaches to the sulcus tympan-

icus of the tympanic bone, where its fibers intermingle with an extensive layer of cavernous tissue.

The tympanic plate of the malleus is firmly attached to the sulcus malleolaris of the tympanic bone by an osseous ankylosis distally, and by a strong fibrous ankylosis proximally. Arising from the inner surface of the anterior leg of the tympanic bone is the lateral malleolar ligament; this ligament is strong and distinct, parallels the outer lamella, and inserts on a small tubercle on the anterolateral surface of the head, at the origin of the neck.

The incudomalleolar articulation is a diarthrodial joint; the articular surfaces of the malleus and incus are congruent and are covered by articular cartilages. In turn, each of these appears to be covered by a layer of fibrous tissue, which blends with the articular capsule peripherally. The capsule is relatively thick and strong in *Tadarida;* this is probably related to the large intra-aural muscles, which place considerable stress on the capsule. The incudostapedial articulation is also typically diarthrodial.

The posterior incudal ligament is similar to that of other Chiroptera in that it consists of a medial and lateral component. Both components are strong and dense; the lateral component is denser than the medial and appears to be a true ligament. The medial component is composed of dense fibrous tissue which does not stain as deeply as that of a typical ligament.

The fibers composing the annular ligament of the stapes are longest anteriorly where they have a length of approximately 0.0175 mm. These fibers gradually decrease in length toward the posterior pole of the footplate, where their average length is approximately 0.013 mm. The ligament is thickest (0.035 mm.) posteriorly; anteriorly it is approximately 0.0175 mm. thick.

There are no suspensory ligaments or folds associated with the ossicles in *Tadarida.*

Intra-aural Muscles: The tensor tympani is relatively large (0.17 cu. mm.) in *Tadarida;* of this volume, 0.086 cu. mm. is muscle and 0.084 cu. mm. is tendon. The muscle has its origin from the sphenoid bone, extensions of the cartilage of the Eustachian tube, and from the pyriform membrane. It lies along the dorsomedial wall of the tympanic cavity, courses across the petrosal bone, and inserts by two tendons into the muscular tubercles on the inner surface of the malleus. The upper tendon and that part of the muscle associated with it are considerably larger than the lower tendon and part of the muscle.

The stapedius muscle is multipennate; it has a length of 1.75 mm., a volume of 0.35 cu. mm., and lies in a small fossa adjacent to the facial nerve. The muscle passes beneath the nerve and is innervated by a branch from it. Within the tendon of the muscle is a small cartilaginous skeletal element of Paauw. The tendon extends beyond this element into the tympanic cavity and inserts into the muscular process on the stapes. The nerve supply to the muscle is seemingly rich (Plate XI); in addition to the branch from the facial nerve, a branch of the glossopharyngeal enters the substance of the muscle.

Eumops perotis

The structures of the middle ear of *Eumops* are similar, in most respects, to those of *Tadarida.*

Tympanic Membrane: The tympanic membrane has a long diameter of 4.4 mm. and a short diameter of 3.3 mm. Its area is approximately 11.5 sq. mm., and the membrane is inclined 50 degrees from the horizontal. The membrane varies in thickness from 0.004 mm. peripherally, to 0.009 mm. centrally.

Malleus: The malleus of *Eumops* (Fig. 29) has a volume of 0.448 cu. mm. The head is more sharply outlined than that of *Tadarida* and shows a more prominent capitular crest and spine. The articular facets are also somewhat different; the superior facet is concave, and the inferior facet is smoothly rounded and is placed medially. Laterally the two facets subtend an angle of 130 degrees; medially, however, the superior facet overhangs the inferior and the two subtend an angle slightly less than 90 degrees. The head has a length of 0.93 mm., a height of 0.75 mm. and a breadth of 0.69 mm. The superior articular facet is low and appears to have less surface area then the inferior; it has a height of 0.25 mm. while the inferior has a length of 0.43 mm.

The anterior process is similar to that of *Tadarida,* except that it is entirely osseous, is reinforced beneath the head by fibrous tissue, and has a more prominent central buttress. The lateral process is prominent and is capped by cartilage. The manubrium is osseous, rather than cartilaginous as it is in most other bats considered in this investigation. It has a length of 2.6 mm. from its tip to the lateral process. The membrane surface is sharp except at the extreme tip, which shows slight spatulation. The sharp margin is thin, flexible, and resembles a mucosal fold.

The obicular apophysis is elongated and has a length of 0.8 mm. The muscular process is a sharp crest on the medial side of the neck

and manubrial base; it is prominent, extends to the lower border of the lamina and is pierced by the chorda tympani nerve.

Incus: The incus of *Eumops* (Fig. 31) has a volume of 0.095 cu. mm. and resembles that of *Tadarida*, except in size and in the shape of the short process. The short process is a conical projection with a wider base than that of *Tadarida;* it has a length of 0.38 mm. The long process has a length of 1.0 mm. and shows a deep sulcus incudis which excavates its entire anterior surface. The pedicle is long and cylindrical, and the lenticular process has long and short diameters of 0.26 mm. and 0.21 mm., respectively.

Stapes: The stapes of *Eumops* (Fig. 30) has a volume of 0.021 cu. mm. The head has long and short diameters of 0.27 and 0.21 mm., respectively. The posterior crus has a length of 0.50 mm. and the anterior crus a length of 0.75 mm. The crura, with the footplate, form the boundaries of a triangular intercrural foramen; the crural sulci are poorly developed throughout. The footplate of the stapes has a long diameter of 0.83 mm., a short diameter of 0.37 mm., and the area of its vestibular surface is approximately 0.225 sq. mm. In other respects, the stapes is identical to that described above for *Tadarida*.

Articulations and Attachments: The annular ligament of the stapes is thickest posteriorly and thinnest anteriorly, and its fibers are longest anteriorly and shortest posteriorly. The thickness of the ligament varies from 0.070 mm. to 0.035 mm.; the length of the fibers around the anterosuperior curvature of the footplate is 0.035 mm., and around the posterior curvature the length is approximately 0.013 mm. Other features of the articulations and attachments are essentially like those described for *Tadarida*.

Intra-aural muscles: The tensor tympani muscle of *Eumops* is long and straight. It has a length of 4.0 mm.; the total volume of the muscle is 0.90 cu. mm., of which 0.217 cu. mm. is muscle and 0.683 cu. mm. is tendon. The muscle takes origin from the dorsal and ventral sides of the posterior extension of the cartilage of the Eustachian tube. It courses along the petrosal bone and inserts by a broad flat tendon into the muscular crest on the inner surface of the neck and manubrial base of the malleus. In one specimen, the tendinous band showed a slight split so that two tendons were present.

The stapedius muscle is relatively large in *Eumops;* its volume is approximately 0.70 cu. mm. The muscle shows a rich nerve sup-

ply, and is similar in all respects, except size, to that of *Tadarida,* described above.

DISCUSSION

The forms considered in this investigation utilize a wide range of frequencies, and can be arbitrarily placed into frequency groups, either on the basis of recent physiological evidence, or, where this is wanting, on basis of accepted taxonomic relationships, habitat and supposed sound field environment. Three basic groups, a low frequency, an intermediate frequency and an ultrasonic, can be established.

The low frequency group is represented by the mole, *Scalopus;* this mammal is almost completely fossorial, spending more than 99 percent of its life in underground tunnels of its own construction (Hall, 1955). Although its auditory frequency range is not known, it does not seem likely that high frequencies would be compatible with the animal's underground environment, in which high frequencies would readily be absorbed.

The hedgehog, *Erinaceus,* represents the intermediate group; this animal is terrestrial and differs from the other forms considered in having relatively good eyesight. It would thus appear to be less dependent on hearing than would the other, essentially blind forms. Sounds important to this animal would not seem to be either in the lower or the ultrasonic range, but rather between these extremes, and possibly similar to those utilized by other small terrestrial forms such as cats or dogs. These animals may be able to hear sound approaching the ultrasonic range, but it does not appear likely that they would have any special acuity or use for such sounds.

Based on physiological data from echolocating bats, all of the Microchiroptera belong in the ultrasonic group. In addition, there is some evidence that shrews and shrew-like mammals may also belong here (Schleidt, 1951). Based on physiological data on the average upper frequencies emitted during a single ultrasonic cry, the bats included in the ultrasonic group can be placed into low and high ultrasonic categories. Although the forms in question can undoubtedly hear higher frequencies than those which are cited, it is assumed that this upper frequency at least provides an index to the high frequency sounds best utilized. Those forms in which the average upper frequency of the ultrasonic pulse (cry) generally lies below 50 kc/sec are included in the low ultrasonic category; placed in the high ultrasonic category are those which utilize an upper frequency above 50 kc/sec.

On this basis, *Eumops*, *Tadarida* and *Plecotus* belong in the low ultrasonic category. The frequencies utilized by *Eumops* appear to lie in the range of 20-40 kc/sec (Novick, personal communication). No values for *Tadarida brasiliensis* are recorded in the literature; other species of *Tadarida*, however, generally produce low ultrasonic pulses below 50 kc/sec (Griffin, 1958; Novick, 1958b). According to Griffin (1958), *Plecotus* utilizes low ultrasonic pulses in the 27-39 kc/sec range.

In the high ultrasonic category are *Glossophaga*, *Natalus*, *Rhinolophus* and *Myotis*. Griffin (1958) cites an upper value of 128 kc/sec for *Glossophaga soricina;* the cry of *Natalus* is also high, and probably has a range of from 60-90 kc/sec, according to some unpublished records of Novick. Möhres (1953) reports that *Rhinolophus ferrum-equinum* utilizes a rather constant pulse of 80 kc/sec. No specific values have been reported for *Myotis velifer;* other species of *Myotis*, however, generally emit an average upper frequency in the range of from 60-90 kc/sec (Griffin, 1958; Novick, 1958b).

According to Griffin (1958), *Eptesicus fuscus* has an average upper frequency of 50 kc/sec, which places this bat at the arbitrary line of division between the low and high ultrasonic categories. The inclusion of *Cryptotis* in the high ultrasonic category is based on evidence presented by Schleidt (1951) who found suggestions that conditioned shrews and other small mammals are aware of sounds often as high as 100 kc/sec.

With the establishment of these frequency groups, the gross and microscopic anatomy of the structures of the middle ear may be analyzed in terms of possible adaptations toward acuity in certain frequency ranges. Thus, morphological patterns appearing consistently in any one group may suggest adaptations toward acuity for the frequency range of that group. Those structures which seem most important in the transfer of acoustical energy across the middle ear are the tympanic membrane, the inter-ossicular articulations and the ligaments and muscles acting on, or in association with, those parts.

The tympanic membrane is fundamentally similar in all forms examined. The manubrium of the malleus is embedded within the pars tensa, enabling vibrations of the membrane to be transferred to the ossicular chain. The fibrous stratum of the membrane is strongly attached to the lateral process of the malleus and, also, to the tip of the manubrium. Weaker, variable attachments of this

stratum occur along the remainder of the border of the manubrium. The degree of spatulation or broadening of the surface of the manubrium related to the tympanic membrane roughly determines the extent or strength of the attachment of the fibrous stratum along this border. *Erinaceus* and *Scalopus*, the two forms included in the nonultrasonic groups, show a broad manubrial surface along the entire length of the process. Forms included in the ultrasonic group do not show equivalent broadening of this surface. A long spatulated tip is present in *Rhinolophus* and *Glossophaga;* manubrial expansion is slight in *Eumops* and *Cryptotis*, and is moderately expressed in the remaining forms. In some of these forms the variability in the degree of spatulation suggests adaptation to ultrasonic transmission. In *Eumops*, for example, only the tip of the manubrium, occupying the umbo, has a firm attachment to the tympanic membrane. The remaining portion of the manubrial border is thin and flexible, almost mucosal in structure. It appears that only those frequencies causing an excursion of the tympanic membrane in the area of the umbo would be transmitted with efficiency. Thus, this particular relationship may be an adaptation toward ultrasonic transmission in *Eumops*, a bat with ossicular structures of a size that does not appear to be well-adapted to ultrasonic perception (see below). The relationship of the manubrium to the tympanic membrane described for *Eumops*, is variably expressed in other chiropteran forms, especially those included in the low ultrasonic category.

In all forms, a strong attachment of the tympanic membrane to the malleus occurs at the lateral process; all of the fibers of the fibrous stratum coming into relationship with this process appear to insert into it. This attachment, in the superior quadrant of the membrane at the border of the pars flaccida, anchors the manubrial base to the membrane and roughly serves as a suspensory support strengthening the connection between membrane and malleus. Its peripheral location makes it unlikely that the attachment is important in the transmission of vibrations; it seems more reasonable to assume that strength at this point accommodates for tensions exerted by the tensor tympani muscle.

An interesting associate of the tympanic membrane is the cavernous tissue, an extensive network of vascular channels lying in the sulcus tympanicus of the tympanic bone among the fibers of the annulus fibrosus. This tissue is a characteristic feature of the tympanic membrane in all Chiroptera examined, but it was not found in any of the Insectivora. The functional significance of this

tissue is not understood, but since it is so intimately associated with the fibers of the annulus fibrosus, it would appear that the amount of blood in these vessels would influence the tension of the tympanic membrane; conversely, the tension of the membrane may influence the degree of filling of the vascular tissue. Except for the presence or absence of this cavernous tissue, the structure of the annulus is similar in all forms considered. It is widest basally and narrowest along the upper margins of the tympanic sulcus, suggesting that the greatest amount of tension is applied to the basal part of the membrane.

The pars flaccida generally occupies the posterior superior quadrant of the tympanic membrane and is associated with the tympanic notch. In the forms considered, this part of the membrane is usually thicker than the pars tensa; the thickness results from either the development of the middle layer of the sustantia propria, which is composed of unorganized collagenous connective tissue rather than circular or radiating fibers like the pars tensa, or, where this is wanting, from the thickening of the stratum cutaneum and/or mucosum. Consequently, this part of the tympanic membrane possesses neither the tension of the pars tensa, nor its ability to follow quick physiological movements (Wolff, Bellucci and Eggston, 1957). In Chiroptera the pars flaccida is small and difficult to recognize in some forms because of reduction of the tympanic notch; the periphery of the pars flaccida, however, lacks the cavernous tissue characteristic of the annulus fibrosus of the pars tensa. In the insectivores, *Erinaceus* and *Cryptotis*, the pars flaccida is large because of a prominent tympanic notch; in *Scalopus*, however, the tympanic bone is fused indistinguishably with the surrounding skeletal elements, and the tympanic notch and associated pars flaccida are difficult to interpret.

The shape and inclination of the tympanic membrane are dependent on the shape and inclination of the tympanic bone. In bats there is a tendency toward a rounded membrane, while in the insectivores investigated, the membrane tends to be more oval. In insectivores the tympanic membrane is generally inclined approximately 25 degrees from the horizontal. In Chiroptera the inclination varies considerably; it is greatest in *Rhinolophus* (82 deg.), *Glossophaga* (70 deg.), and *Natalus* (60 deg.), three representatives of the high ultrasonic category. Because of this it might be suggested that approach of the tympanic membrane toward a more vertical position is advantageous to ultrasonic acuity in

Chiroptera. *Myotis*, however, also a member of the high ultrasonic category, has an inclination of only 45 degrees, less than that of the bats considered in the low ultrasonic category. In the latter group, the inclination of the membrane is consistently in the range of from 50-55 degrees. The relatively close taxonomic relationship of forms in the low ultrasonic category suggests that taxonomic relations are a significant factor in inclination of the membrane. With the study of more forms, this point may become clear.

The factors governing inclination of the tympanic bone and the associated tympanic membrane are the inflation of the cochlea, and the enlargement of the space between the ventromedial part of the tympanic bone and the undersurface of the petrosal (Van der Klaauw, 1931). Although both of these factors appear to influence inclination of the tympanic bone in Chiroptera, the great degree of inclination in *Rhinolophus* can be attributed almost entirely to the inflated cochlea; in other forms, however, cochlear inflation does not seem to be as important as development of the space between the medial border of the tympanic and the undersurface of the petrosal, and associated development of an entotympanic element. This is especially evident in the figures given for cochlear volume and tympanic inclination in Table 1; there it can be seen that *Tadarida* and *Glossophaga* are bats of approximately equal size, yet *Tadarida* has a cochlear volume of 4.5 cu. mm. and an inclination of 50 degrees, while *Glossophaga* shows an inclination of 70 degrees and a cochlear volume of only 1.45 cu. mm. Comparing this with other values cited, it does not seem that inclination of the tympanic membrane, or cochlear volume, can at this time be correlated with the ability to transmit or receive ultrasonic sounds; with the study of more forms, however, it may be found that a relatively vertical tympanic membrane is advantageous to ultrasonic transmission, as is suggested in the three high ultrasonic forms already considered (*Rhinolophus*, *Glossophaga* and *Natalus*).

It seems that a small tense tympanic membrane is best suited to efficient transmission of ultrasonic vibrations. *Natalus*, *Glossophaga*, *Rhinolophus* and *Myotis*, members of the high ultrasonic category, all have small tympanic membranes with areas of 1.2, 2.4, 2.5, and 2.4 sq. mm., respectively (Table 2). On the other hand, those bats in the low ultrasonic category show membranes generally of a size greater than 4.0 sq. mm. in area. *Eptesicus*, utilizing frequencies which place it between the low and high ultrasonic categories, has a tympanic membrane measuring 3.0 sq. mm. in area. Although

the tympanic membrane of *Eumops*, a low ultrasonic form, is larger than that of *Scalopus*, a low frequency form, it seems that this apparent discrepancy may be disregarded, for the mole has modified other parts of the middle ear in the direction of low frequency acuity. The large tympanic membrane of *Erinaceus* (20.3 sq. mm.) supports its placement in the nonultrasonic group; likewise, the small tympanic membrane (1.9 sq. mm.) in *Cryptotis* supports the assumption that this form is properly placed with the ultrasonic group.

In general terms one might expect the size of the tympanic membrane to be more or less proportional to the size of the animal. As in the case of ossicular size (see below), this assumption finds some support in the consideration of closely related forms; even here, however, as in widely divergent forms, consistent relationships between the size of the animal and the size of its tympanic membrane may not exist. *Natalus*, *Myotis*, and *Glossophaga* are among the smallest forms considered, and it is in these that we find the smallest tympanic membranes. *Natalus* is approximately half the size of *Glossophaga* and has a tympanic membrane approximately half the size of that of *Glossophaga*. *Tadarida*, on the other hand, is about the same size as *Glossophaga*, yet has a membrane twice as large.

The relatively large size of the tympanic membrane in some small mammalian forms has been commented upon by several authors (Wilkie, 1925, 1926; Howell, 1932; and others), and emphasized by comparisons to the size of the tympanic membrane in large animals. Gaughran (1954) cites the following figures given by Wilkie (1925, 1936): ox 12.5 by 11 mm., horse 11 mm. in length, and domestic sheep 9 x 7 mm. In comparison, *Talpa* and *Scalopus* have membranes measuring 4 x 3.5 mm. (Wilkie, 1925; Gaughran, 1954), or 10.8 sq. mm., as cited here. To this can be added *Eumops* (12.5 sq. mm.), *Erinaceus* (24.2 sq. mm.) and others (Table 1). From these data, as various investigators have stated, it is apparent that the size of the tympanic membrane in these small mammals is relatively large when compared to the size of the membrane in large domesticated mammals. It certainly seems more reasonable, however, to say that the tympanic membrane is small in these large domesticated forms. For example, if a small mammal the size of a shrew, were to evolve into an animal the size of a horse, and if the size of the tympanic membrane evolved proportionately, then the horse-sized animal should have a tympanic membrane

at least 70 mm. in length; conversely, the membrane in the shrew-sized animal should be only 0.3 mm. in length if proportional to the size of the tympanic membrane of a horse. This is, obviously, not the case, for the tympanic membrane in the horse is actually only two or three times greater in size than is the membrane in some of the smallest mammals. If size and thicknes of the tympanic membrane are related to the frequencies the membrane is capable of transmitting, it is logical that the size of the membrane cannot be expected to be proportional to the size of the animal. In other words, if the size of the tympanic membrane is adequate for the perception of sounds within a common useful range to begin with, it would be of little value to alter radically the size of this structure in the evolution of a small form to a large one. Thus, in keeping the membrane confined to proportions suitable to the frequencies utilized, undue modification of other structures associated with the auditory system would not need to follow.

Although a small tympanic membrane seems well adapted to transmission of ultrasonic sounds, tympanic membranes of larger size can undoubtedly transmit a wide range of frequencies. The auditory acuity of given animals for these frequencies may, however, vary considerably since the tympanic membrane is only a small part of the mechanical system concerned with the transmission of vibratory energy across the middle ear. The mechanical efficiency produced by the remaining structures of the middle ear would seemingly have considerable bearing on the stimulus which ultimately reaches the inner ear, and consequently, on the resulting auditory acuity of the animal for certain frequencies.

One method commonly employed in calculating at least part of the mechanical efficiency in the transfer of energy from the external auditory meatus to the fluid of the cochlea invloves determining the ratio of the area of the vestibular surface of the footplate of the stapes to the area of the tympanic membrane (Table 1). In some of the insectivores (*Cryptotis, Blarina, Sorex* and *Erinaceus*) the area of the tympanic membrane is approximately 60 times larger than that of the footplate. Scalopus, however, shows a ratio of only 14:1 (19:1 according to Gaughran, 1954). Representatives of the Chiroptera, on the other hand, generally show a high ratio, ranging from as low as 16:1 in *Natalus*, to as high as 53:1 in *Tadarida*. In man the ratio is approximately 20:1 (Best and Taylor, 1943) or 27:1 (Munson, 1950). The data thus gathered are not only variable, but difficult to interpret. Some degree of mechanical

advantage is necessary to overcome the friction of the ossicular system; it may be noted that in those forms (*Erinaceus, Cryptotis,* and *Eumops*) which fall into the ultrasonic and intermediate frequency groups, where energy loss through friction would seem to be of some significance, (indicated by the nature of the incudomalleolar articulation and the nature of the ligaments associated with the ossicular chain, see below), the ratio of the area of the footplate to that of the tympanic membrane is high (ca. 60:1). In *Scalopus* and man, essentially low to intermediate frequency utilizers, energy loss to friction is probably greater, and the ratio is low. Thus, in these latter forms high frequency and ultrasonic vibrations would be transmitted with little efficiency through the ossicular chain.

Another consideration which must not be overlooked, is that oscillations of the auditory ossicles can be attenuated by reflex contractions of the tensor tympani and stapedius muscles (Munson, 1950). In this respect, it may be of some significance that in the insectivores the intra-aural muscles are poorly developed, relative to those in bats, and the ratio between the area of the stapedial footplate and that of the tympanic membrane is high, approximately 60:1. In bats, on the other hand, the intra-aural muscles are well developed, and the ratio is lower. Among bats, however, there appears to be no correlation between this ratio and the degree of development of the tensor tympani and stapedius muscles.

Additional mechanical advantage in the system can be computed employing measurements of several parts of the ossicular chain which act as lever arms. If the middle of the incudomalleolar articulation is taken as the point of rotation, and considered to be a fulcrum, then the ratio of the length of the malleolar lever arm to that of the incudal arm expresses a mechanical advantage. In the laminated type of malleus, characteristic of the forms included in this investigation, the length of the malleolar lever arm is equal to the sum of the lengths of the manubrium, manubrial base, and the length of the neck as far as the midpoint of the incudomalleolar articulation. The length of the incudal lever arm is equal to that length of the incus which extends from the midpoint of the malleoincudal articulation to the tip of the long process. In the nonlaminated type of malleus, such as that in man, the length of the malleolar lever arm is equal to the length of the manubrium plus the additional distance to the midpoint of the incudomalleolar articulation. Here, the length of the incudal lever arm is computed in the same manner as in forms having a nonlaminated or neckless

malleus. The greater the resultant ratio, the greater is the effect of strengthening vibrations, decreasing their amplitude, and producing a mechanical advantage best suited for the transfer of high frequency sound (Cockerell, Miller and Printz, 1914). Ratios calculated in this manner for the forms included in this investigation are shown in Table 1. In general, it appears that the ratio is highest in forms included in the high ultrasonic category; these show ratios ranging from 5:1 in *Natalus* to 4:1 in *Glossophaga, Rhinolophus,* and *Cryptotis.* The forms included in the low ultrasonic category show a range of from 3.6:1 in *Plecotus* to 3:1 in *Tadarida. Scalopus,* representing the low frequency group, has a ratio of only 2.2:1. On the other hand, *Erinaceus,* of the intermediate frequency group, has a high ratio of 4.6:1. Thus, except in *Erinaceus,* there seems to be a good correlation between this ratio, the known frequencies utilized, and the presumed range of auditory sensitivity in the several forms considered. The ratios of these ossicular lever arms, and the mechanical advantages produced, are largely dependent on the structure of the individual ossicles.

The mammalian malleus (Fig. 1) has three primary structural parts, a manubrium embedded within and attached to the tympanic membrane, a head articulated with the incus, and an anteriorly-projecting mass of bone which anchors the malleus anteriorly and supports the ossicular chain. A fourth structure, often reduced and sometimes absent in specialized forms, is the neck of the malleus.

The anteriorly-projecting mass of bone may be simply expressed as a short, cylindrical spine extending anteriorly from the manubrial base and providing an area of attachment for the anterior malleolar ligament. This expression of form is usually associated with mallei having short necks, such as those of man and other primates. In "lower" mammalian forms, the neck of the malleus tends to be long and is usually supported by a thin bony plate, the lamina. In some insectivores, bats and rodents, the malleolar neck is extremely long and curved. In mallei of this type the lamina is often broad and complex in structure; the entire projection may be marked by variously-developed ridges, thickenings, and grooves. The names given in the literature to those bony landmarks are often as variable and confusing as the structures themselves.

In mallei with well-developed laminae the distal end of the anteriorly-projecting mass of bone lies in the sulcus malleolaris of the tympanic bone, and is attached there by an osseous or fibrous ankylosis. This part attaching to the tympanic bone has been consistently recognized by the term "anterior process," or by the

synonymous terms processus gracilis, folianus, or longus. These terms have apparently been derived by using the human malleus as a basis for comparison. This process in "primitive" mammalian forms does not, however, resemble the anterior process of human anatomy in shape, position or mode of attachment. On the other hand, a thickened, inferior border of the lamina, which extends forward from the manubrial base and is accompanied on its medial surface by the chorda tympani nerve, closely resembles the anterior process of the human malleus. This border has previously been recognized as representing the anterior process of the human malleus (Doran, 1878; Cockerell, Miller and Printz, 1914), but this presumed homology is often overlooked. The inferior border of the lamina blends with the undersurface of a plate of bone attached to the tympanic bone; some investigators (Gaughran, 1954; Cockerell, Miller and Printz, 1914) imply that the free border of the lamina represents the proximal part of the anterior process, but consider the bony plate to be the distal part of the anterior process. This plate, however, seldom lies in the same plans as the lamina, and the border, therefore, seldom appears to represent the proximal part of this plate, or anterior process, as they call it. The proximal representation of the plate appears to lie along the upper border of the lamina in most cases, and is represented there by a medial and/or lateral "shelf" of bone. In his descriptions of the malleus, Wassif (1948) recognizes these shelves as the inner and outer lamellae of the anterior process. Thus, practically every border and process associated with the lamina has been called "anterior process."

In the hope of offering a rational solution to this problem of nomenclature, the entire complex, including lamina, has here been called anterior process, and the various prominences, ridges, and grooves found in relation to it are considered to be parts of the anterior process. The tympanic plate is that part attaching to the tympanic bone; the proximal parts of this plate are the inner and outer lamellae (Wassif, 1948); and the longitudinal groove or depression formed at the union of these two lamellae is the interlamellar sulcus. The inferior border of the lamina, presumably homologous to the anterior process of human anatomy, is the pars processus anterioris, and the central thickening of the lamina is the central (laminar) buttress (median buttress of Wassif, 1948). In some forms the upper border of the lamina is strongly supported by a mass of bone continuous with the head of the malleus; this mass

has been called the cephalic process of Cockerell, Miller and Printz (1914), but is here considered a thickened outer lamella.

In insectivores the tympanic plate shows a looser attachment to the tympanic bone than it does in Chiroptera; this attachment is generally a fibrous ankylosis in the former and an osseous ankylosis in the latter. This attachment of the tympanic plate to the tympanic bone provides one of the strongest supports of the ossicular chain. In Chiroptera, where this attachment of tympanic process to tympanic bone is an osseous ankylosis, there are no suspensory ligaments associated with the head of the malleus or the body of the incus. In insectivores, however, where this articulation is a fibrous ankylosis, typical suspensory folds or ligaments are present. The strong osseous union between malleus and tympanic bone in bats gives more rigidity to the ossicular complex than can be attained by the looser fibrous attachment in the insectivores; this rigidity of the ossicular complex certainly seems advantageous for the transfer of ultrasonic vibrations.

The inner and outer lamellae of the anterior process, which extend distally to form the tympanic plate, differ markedly in the various genera of insectivores and bats. In most Chiroptera the outer lamella has a thickened margin which, with the upper border of the lamina, merges with the anteroinferior surface of the head of the malleus. In the Molossidae (*Eumops* and *Tadarida*), however, the outer lamella is an oblique, thin, osseous plate lying along the upper border of the lamina, and it attaches rather broadly to the head of the malleus. In bats the inner lamella is usually narrow proximally, broad distally and thin throughout, and is pierced by the chorda tympani nerve. The inner lamella merges with the head of the malleus in *Glossophaga, Natalus,* and *Rhinolophus.* In *Myotis, Eptesicus* and *Plecotus* (Vespertilionidae) it attaches weakly to the head, or merges with the outer lamella so that both lamellae join the head as a single unit. In *Tadarida* and *Eumops* (Molossidae) the inner lamella terminates abruptly just inferior to the anteromedial surface of the head, and has no direct connection with the head. In these Molossidae the inner and outer lamellae are almost mirror images of one another; they merge with the upper border of the lamina and form a deeply-cut interlamellar sulcus, V-shaped in cross-section. In other bats the interlamellar sulcus tends to be broadly U-shaped in cross-section.

In the insectivores, *Erinaceus, Cryptotis* and *Scalopus,* both the inner and outer lamellae of the anterior process are strongly joined

to the head of the malleus. In *Cryptotis,* the lamellae merge with the undersurface of the head, and, thus, roughly resemble the lamellae of some Chiroptera (*Glossophaga, Natalus, Rhinolophus*). In *Erinaceus* both lamellae merge with the anterior surface of the head; the outer lamella is thickened proximally where it merges with the head. In *Erinaceus*, and to a lesser degree in *Scalopus*, this proximal portion appears to be comparable to that part which Cockerell, Miller and Printz (1914) call the cephalic process in mallei of rodents. The inner lamella is thick in those forms in which it merges with the head, but not as thick as the outer lamella. In *Scalopus* the outer lamella cannot be distinguished from the upper border of the lamina. The inner lamella merges broadly with the head in a plane parallel to that of the lamina; its lower portion curves inward to meet the lamina and, thus, an elaborate deep interlamellar sulcus (cavum laminae of Stroganov) is formed. This inner lamella appears to be homologous to the inner lamella of other forms considered, since the chorda tympani nerve and its lamellar foramen are in a position comparable to that seen in forms in which the inner lamella is clearly distinguishable.

The axis of rotation in laminated mallei roughly runs in a line corresponding to the longitudinal juncture of the inner and outer lamella of the anterior process with the lamina of this process. Rotation about this axis, however, is limited because of the osseous structure of the anterior process and because of its strong union with the tympanic bone. Any rotation that occurs is seemingly accomplished through torsion along the line of juncture of the tympanic plate and lamellae with the lamina. The greatest amount of torsion is probably applied by the tensor tympani muscle, while lesser degrees could result from sound vibrations. The presence of fibrous connective tissue situated on either side of the lamina along this line of juncture, supports the suggestion that this area is subject to torsional forces. This fibrous supportive tissue appears to be supplemented periosteum; it is not present in all forms, but is usually well marked in those forms with large tensor tympani muscles. Support against torsional forces applied to the lamina is seemingly provided by this fibrous tissue. In addition, the lamina is further supported superiorly by the lamellae. The pars processus anterioris seemingly functions as a support of the inferior border of the lamina. This part of the anterior process is developed in *Eptesicus, Myotis,* and *Plecotus* (Vespertilionidae), and in the insectivore, *Erinaceus;* it is less prominent, or absent, in other forms

considered here. In none of the forms examined was this thickening found to extend along the entire inferior border of the lamina to its junction with the undersurface of the tympanic plate; this feature also suggests that torsion occurs along the line of juncture of the lamina with the lamellae and tympanic plate.

Supporting the central portion of the lamina is the central buttress. Like the pars processus anterioris, this part of the anterior process is well developed in some forms, but poorly developed in others. This buttress was not noted in any of the insectivores; *Cryptotis,* however, has a modified central region in the lamina, which appears as a bend and could, in effect, subserve the same supportive function as the central buttress of other forms. There is some evidence that the development of the central buttress is related to the development of other laminar supports, particularly the pars processus anterioris. In the Vespertilionidae (*Myotis, Eptesicus* and *Plecotus*) the pars processus anterioris is well marked, as noted above; the central buttress, however, is poorly represented. In *Glossophaga* and *Natalus* the pars processus anterioris is wanting; the central buttress, however, is well developed and involves the greater part of the lamina.

Although the central buttress and the pars processus anterioris support the lamina, the lamina itself, as it extends between the head and neck superiorly and the neck and manubrial base posteriorly, serves as an important structural support for the entire malleus, since it essentially binds all these parts into one functional unit. Were it not for this support, the integrity of the entire element would be taxed, especially because of the long curved neck. The relationship of neck length to the size of the lamina appears to be consistent, for mallei with long necks invariably seem to be of the laminated type, while mallei with no necks, or only short ones, generally show only an anterior process.

The shape of the neck is, except in *Scalopus,* similar in all forms considered here. It is long and sigmoidal in the Chiroptera and many of the Insectivora, although neither Doran (1878) nor Wassif (1948) makes a special point of this character. On the internal surface of the neck, usually close to the manubrial base, is the processus muscularis for the insertion of the tensor tympani muscle. In those forms in which this appears as a single tubercle, it is separated from the manubrial base by a notch or groove formed by the chorda tympani nerve. This muscular process may be represented by a crest or by two tubercles; these variations generally

indicate the type of insertion made by the tensor tympani muscle, and suggest, respectively, either a broad flat insertion, or an insertion by two tendons.

The term manubrial base has here been applied to the relatively massive area between the neck and the manubrium. In the Chiroptera, and in *Erinaceus* and *Cryptotis* (Insectivora), the area has associated with it the orbicular apophysis, the lateral process, and, when present, the basal part of the pars processus anterioris.

The orbicular apophysis is a peculiar structure of unknown significance. It occurs in many insectivores, bats and rodents (Doran, 1878; Cockerell, Miller and Printz, 1914) as a prominent process, which assumes a wide variety of shapes and forms. In most of the forms studied in this investigation, two structures, the chorda tympani nerve and posterior malleolar fold, are usually associated with it. Whether or not these have any bearing on its development is difficult to ascertain, but it appears doubtful. It is suggested, as a speculative possibility, that this bony mass may function as a ballast.

The lateral process is present in all forms, although it is seldom conspicuous. Composed of cartilage, or capped by cartilage, it provides an area for the insertion of fibers of the stratum fibrosum of the tympanic membrane. The process is peculiarly developed in *Scalopus*, in which it appears as a sharp spine projecting prominently into the tympanic membrane. Gaughran (1954) has, in *Scalopus*, called this the "orbicular apophysis," but observations in this study clearly indicate that it is the lateral process, because of its relationship to the basal part of the manubrium and to the tympanic membrane. No distinct orbicular apophysis can be recognized in *Scalopus*; in those forms in which it is present, it does not contact the tympanic membrane.

The manubrium of the malleus is generally saber-shaped with the inner border thickened. In insectivores the manubrium is osseous; bats invariably show a manubrium composed largely of cartilage, but, in some forms, the thickened inner border is ossified. Spatulation of the manubrium is a constant feature and appears to be related to the attachment of the stratum fibrosum of the tympanic membrane. In all instances the firmest attachment is at the tip of the manubrium where spatulation is broadest. In *Erinaceus* and *Scalopus* the entire external border of the manubrium is broad, while in *Cryptotis* only the tip is broadened into a spatulation while the remaining part of the border appears as a sharp edge. In *Glosso-*

phaga and *Rhinolophus* (Chiroptera) the manubrium is broadened along its entire external border, while other Chiroptera show broadening or spatulation involving only the distal third or half of the manubrium. In *Eumops* only the tip is spatulated; the remaining edge is thin and flexible and has the appearance of a thickened mucosal fold. These variations are difficult to explain; no correlation between manubrial spatulation and the frequencies utilized, the size of the tympanic membrane, the length of the manubrium or the volume of the tensor tympani can be established at this time. With a structural arrangement such as that described in *Eumops*, it would appear that vibrations of the tympanic membrane at the umbo (presumably high frequency vibrations) would be those most efficiently transferred to the malleus.

The transfer of vibrations from malleus to incus involves the articulation of the head of the malleus with the body of the incus, the incudomalleolar articulation. Of some importance in relation to these parts, and to the joint, are the shape of the head and articular facets and the ligaments associated with them. The ligaments related to the head are the lateral malleolar ligament and the suspensory ligaments or folds. The lateral malleolar ligament arises from the anterior leg of the tympanic bone and attaches to the anterolateral part of the head; it seemingly limits lateral rotation of the head resulting from contraction of the tensor tympani muscle. This ligament is strong, small and discrete in bats; in insectivores it is fibrous, but is poorly organized and developed. The suspensory ligaments, or folds (which appears to be a better term since they are usually reflections of mucous membrane) are usually absent in the bats but are well developed in the insectivores. As previously stated, this development of suspensory folds in insectivores may be related to the type of attachment of the tympanic plate of the anterior process to the tympanic bone.

The articulation between the malleus and the incus is a diarthrodial joint in all forms investigated; the articular surfaces are cartilaginous, and a well-developed, but delicate, capsular ligament is present. The articular surfaces of the malleus and incus are generally mirror-images of one another, therefore, only the malleolar articular surface has been considered in detail. In Chiroptera the superior and inferior articular facets form a more acute angle than they do in the insectivores. From figures and descriptions of the malleus in monotremes (Huxley, 1869; Doran, 1878) and marsupials (Doran, 1878; Wassif, 1948), and from descriptions of the ossicles of gen-

eralized insectivores, such as the Erinacidae and Soricidae (Doran, 1878), it appears that, primitively, the head of the malleus was small, flat and had a broad articular surface. In the insectivores, *Erinaceus* and *Cryptotis,* the angles formed at the junction of the superior and inferior articular facets are 140 and 130 degrees, respectively; in *Scalopus* the two facets are approximately in a single plane (180 degrees). In the Microchiroptera, however, the angles formed are considerably more acute, generally ranging between 90 and 100 degrees, except in *Eumops* (130 degrees) and *Plecotus* (68 degrees). Thus, in a broad sense, it seems that these two facets meet at a more acute angle in the mallei of forms considered to be in the ultrasonic frequency group than they do in the forms included in the nonultrasonic group.

It is suggested that an acute angle between these facets permits the joint to be locked more firmly than would be possible in the case of relatively flat articular surfaces. This condition seems favorable to transmission of high frequency vibrations in that the amount of energy lost through friction would be lessened. In the same sense, it would appear that a small joint would favor transmission of high frequency vibrations. A small joint, capable of being tightly locked is present in all of the Microchiroptera, and those forms included in the high ultrasonic category show smaller articular surfaces than do those in the low ultrasonic category. Conversely, those forms in the nonultrasonic groups have comparatively larger articular facets and looser joints. Factors responsible for the tightness of the joint are the capsular ligament, the tension applied by the tensor tympani muscle, and the external pressure applied to the tympanic membrane by atmospheric pressure (Stuhlman, 1952). The capsule and the syndesmosis between the malleus and the long process of the incus are generally tight owing to the elastic qualities of many of their fibers. The intra-aural muscles will be considered later, but it may be said here that they are large in the Chiroptera; the tension applied by these tightens the joint and, presumably, favors high frequency transmission.

Temporary low tone deafness resulting from rapid changes in atmospheric pressure would seem to be a special problem for the bat. In most mammals, swallowing is required to equalize air pressure between the external and middle ear; such a requirement would seem incompatible with echolocation in which the animal continuously sends out ultrasonic cries. It appears that bats may have overcome this problem in two ways; first, by the

utilization of ultrasonics, which are least affected by pressure differences; and, secondly, in some bats the auditory tube has been modified, and may remain open most of the time. Modification of the auditory tube and its related structures has not been considered extensively during this investigation, but has been noted in several forms, particularly *Glossophaga* and *Natalus*.

Since it is suggested that contractions of the intra-aural muscles "tune" the ossicular complex for ultrasonic transmission, every ligament of the complex is seemingly involved and of considerable importance; this may account for the discrete form of all ligaments in the Chiroptera, in contrast to the less-discrete form of the ligaments in the insectivores, in which "tuning" seems less important.

One of the most variable ligaments associated with the ossicular chain is the posterior incudal ligament, which seems to form a main suspensory support for the chain. The structure of this ligament differs in each representative of the three families of insectivores, and differs among representatives of the five families of Chiroptera investigated. The ligament arises from the walls of the fossa incudis and attaches to the tip and sides of the short process of the incus. In *Erinaceus* (Fig. 32) the tip of the short process of the incus is entirely cartilaginous, fits into an elaborated incudal fossa, and is firmly attached there by a mass of fibers which completely envelop it; in addition, a strong ligamentous band of fibers and a synchondrosis add to the rigidity of the articulation. This type of joint would seemingly allow very limited movement in any one direction, probably no more than that which torsion of the cartilage would allow. In *Cryptotis* (Fig. 33) the posterior incudal ligament is single and extends from the roof of the reduced incudal fossa to the tip of a small cartilaginous tubercle equivalent to the short incudal process. This type of articulation appears to provide a more freely movable joint than that observed in other forms. In *Scalopus* (Fig. 34) the posterior incudal ligament is double, and closely resembles the ligament found in bats. This condition in *Scalopus* differs from that described in *Talpa;* according to Wilkie (1929) the articulation is diarthrodial in the latter form.

Variations in the posterior incudal ligament in bats are mainly histological. The lateral component is invariably strong, dense and typically ligamentous. The structure of the medial component of the ligament in *Rhinolophus* is essentially like that of the lateral component; in all other forms examined, the medial component is distinctly less dense than is the lateral. It seems that the bipartite

condition of the ligament would allow some upward displacement of the tip of the short process, but, on the other hand, would limit medial and lateral rotation. The space between the surface of the short process and the roof of the fossa incudis is seemingly large enough to eliminate the possibility of contact between these structures, except (possibly) in *Glossophaga.* In the latter form the roof of the fossa is filled with dense submucous connective tissue, rather than being covered only by a thin mucosal lining such as is present in other bats. In addition, the space between the short process and the roof of the fossa is small, and a sesamoid cartilage is present just beneath the mucous lining of the fossa; this strongly suggests that contact does occur.

It appears that the tensor tympani muscle places considerable tension on the lateral component of the posterior incudal ligament. This possibly accounts for the dense ligamentous organization of this component. The discreteness of the ligament, coupled with the well-developed tensor tympani muscle in bats, suggests a functional importance of these structures in "tuning" the complex for ultrasonic transmission. A looser and/or broader articulation, such as those in *Erinaceus* and *Cryptotis,* subserves the same supportive function, but probably does not have the same degree of the "tuning" function suggested for the Chiroptera. Although the posterior incudal ligament in *Scalopus* bears a striking resemblance to the same ligament in the Chiroptera, its strength can probably be attributed to the massiveness of the ossicular chain which it supports. The size of the ossicles, absence of the tensor tympani muscle, extensive attachment of the malleus to the tympanic membrane, and looseness of the articulations all point to adaptation for transmission of low frequency vibrations.

The position, size and structure of the processes of the auditory ossicles have been mentioned in the consideration of mechanical lever arms and the resultant efficiency of the complex in high frequency transmission. Apparent modification of structure and position of ossicular parts is marked in structures forming the terminal part of the ossicular complex, especially in the long process of the incus and the crura and footplate of the stapes. The long process of the incus roughly parallels the neck of the malleus in *Cryptotis* and *Erinaceus,* and is slightly longer than the horizontal extent of the neck of the malleus. In *Scalopus* the long process diverges from the neck; in Chiroptera it converges toward it and is of approximately the same length.

In *Erinaceus* the long process is solid and flattened, and usually does not show a longitudinal groove along any of its surfaces. This seems to be characteristic of the Erinacidae, since grooving is not present in *Hamechinus auritus, Paraechinus dorsalis* (Wassif, 1948) or in *Gymnura rafflesini* (Doran, 1878). In one set of ossicles from *Erinaceus,* a groove was observed on one surface of the long process of the incus; this groove, however, appears to be a vascular depression and probably represents an individual variation. In *Cryptotis* the long process tends to be cylindrical and lacks longitudinal grooving. This seems to be characteristic of the Soricidae, for the same features were noted in *Blarina brevicauda* and *Sorex cinerius* and, according to Wassif (1948), the same holds true for *Crocidura religiosa.*

In *Scalopus* the long process of the incus has a deep well-marked concavity, the sulcus incudis, which extends along the greater length of the process. In the Chiroptera a similar sulcus is present and is moderately expressed in most forms. In *Eumops* and *Tadarida* this sulcus is particularly prominent and gives the long process an appearance like that of a dugout (piroque). The significance of this sulcus is not clear. According to Wassif (1948:181):

> In some bats and murine rodents the crus longum of the incus lies very close to the neck of the malleus, the proximal part of which seems to fit into the longitudinal groove on the crus longum, thus creating an additional articulation between the incus and the malleus. Doran (1878, p. 488) has already referred to the fact that the incus of *Echidna* is articulated to the malleus by its whole inner surface including the greater part of the long crus. The condition found in *Echidna* appears to be recapitulated to a lesser or greater degree in Marsupials as well as in some Placentals.

As Wassif suggests, this sulcus incudis may be a remnant of the articulation between the neck of the malleus and the long process of the incus. The marked development of the sulcus in some forms where this articulation is not present, does not, however, support this idea, and in none of the forms examined in this investigation is any part of the sulcus an articular surface, as Wassif infers. A syndesmosis between the malleus and the incus is moderately developed in *Erinaceus* and *Cryptotis,* and to a lesser degree in bats. This articulation appears to be formed by extensions of the fibers of the capsular ligament onto the long process of the incus. In spite of the fact that this longitudinal grooving of the long process appears in many "primitive" mammals, it does not appear to be consistent in size, shape or position; a groove similar to the sulcus incudis

has been noticed on the upper surface of the long process of the incus in *Didelphis*. Therefore, evidence for regarding it, or any other sulcus, as a primitive feature does not seem conclusive. These sulci appear, on the other hand, to be an adaptation toward decreasing the mass of the ossicle without sacrificing its strength. For example, in the Molossidae (in which structures of the middle ear are relatively large) were it not for extreme development of the sulcus incudis, it seems that the mass of the incus might well be too great to favor transmission of ultrasonic vibrations.

The distal end of the long process of the incus bears the cartilaginous lenticular process, which occupies the end of a small osseous pedicle. This process articulates with the head of the stapes, forming a small diarthrodial joint, which has a delicate, somewhat loose, joint capsule. Its articular surface is generally smaller than that of the head of the stapes, and allows some gliding and rotatory movements to take place in response to contractions of the intraaural muscles. On the premises that the lenticular process (Sylvian apophysis) is formed from the proximal end of the hyoidean arch and that it is separated from the long crus (long process) during an early stage of development, Doran (1878) assumes that it would be correct to consider it an epiphysis of the incus.

In some forms, especially in *Scalopus*, a distinct slip from the tendon of the stapedius muscle attaches to the articular capsule of the incudo-stapedial joint. The position of the muscular process, close to the head of the stapes, suggests that fibers from the tendon of the stapedius muscle may intermingle with those of the capsule in many forms; this, however, could not be shown in most of the serial sections prepared for this study because the plane of section was unsuited to its demonstration. A similar small slip from the tendon of the stapedius muscle has been described in *Talpa* (Wilkie, 1929) and in man (Wolff, Bellucci, Eggston, 1957; and others). In these forms, and in those considered here, the morphological association of the tendon of the stapedius muscle with the articular capsule permits the joint to be closely coupled during contraction of the stapedius muscle. This probably reduces energy loss through friction and, consequently, seems advantageous to the transfer of high frequency and ultrasonic vibrations. In addition, the slip from the tendon supports and gives added strength to the posterior part of the joint capsule where antagonistic tension applied by the tensor tympani muscle is probably expressed.

The incudo-stapedial articular capsule inserts into the pedicle

of the long process of the incus and into the undersurface of the head of the stapes. A capsular groove is usually not distinct on the stapes, and the narrow constricted pedicle appears to serve as a capsular groove on the long process of the incus.

The stapes is the most variable of the three auditory ossicles. Common features encountered in all forms are a cartilaginous articular surface for the incudostapedial articulation, an intercrural foramen which transmits the stapedial artery, a peripheral cartilaginous labrum of the footplate into which the fibers of the annular ligament insert, and two crura which, with the footplate, bound the intercrural foramen.

In insectivores the crura curve markedly and circumscribe a circular or oval intercrural foramen, while in the Chiroptera the crura are straighter and form two boundaries of a triangular intercrural foramen. The crura are roughly cylindrical in the insectivores and the intercrural surfaces are free of sulci, except in *Cryptotis* where an incomplete sulcus is present on the posterior crus. In the Chiroptera the intercrural surface of each crus generally shows a crural sulcus which, in some forms, is extensively developed, invades the stapedial head and imparts a shell-like appearance to the head of the ossicle. The latter condition is best expressed in *Myotis, Natalus, Glossophaga* and *Rhinolophus.* Factors responsible for development of this sulcus are not apparent, but its presence results in reduction of the mass of the ossicle without alteration of its size or strength. It is interesting to note that forms in which the sulcus is best developed are in the high ultrasonic group, exclusively.

Another difference in stapes of bats and insectivores is found in the nature of the union of the crura with the footplate. In insectivores the crura merge along the long axis of the footplate and usually form a crest, the crista stapedis. In bats the margins of the crura encompass the margins of the footplate at their union with its cartilaginous rim. In prepared dried skulls this union is weak, and the footplate and crura easily separate during attempts to remove the ossicle.

The footplate of the stapes is osseous in the insectivores, including *Cryptotis,* the smallest form considered. In Chiroptera the footplate is often fibrous; the central part of the footplate resembles a membrane stretched across the inner (deep) part of the area circumscribed by the cartilaginous labrum. Thus, in bats, the stapedial crura and footplate are greatly modified and delicate.

Keen and Grobbelaar (1941) have stated that minute auditory ossicles ". . . are clearly useless for a complicated sound conduction process, and may be looked upon as vestigial structures." These investigators were probably unaware that many forms having minute ossicles utilize ultrasounds. The small size of auditory ossicles, however, would not seem to hinder the transmission of low frequency vibrations. Furthermore, the well-developed intra-aural muscles and the nature of the tympanostapedial syndesmosis does not support the assumption that these ossicles are vestigial structures in any sense of the word. On the contrary, they must be interpreted as highly specialized structures.

The fibers of the annular ligament of the stapes are generally longer anteriorly than posteriorly, and the thickness of the ligament is greater posteriorly than anteriorly; this suggests that the greatest stress is placed on the posterior fibers by the stapedius muscle, while the relatively longer anterior fibers allow for greater excursion of the anterior part of the footplate during its transfer of vibrations to the fluids of the inner ear. The length of the fibers of the annular ligament shows a relation to the size of the stapes and to the high frequencies utilized. Thus, in high ultrasonic forms fibers of the ligament are short, and in forms with larger ossicles (low ultrasonic and non-ultrasonic) the fibers of the ligament are longer. No correlation was found to exist between the size of the stapedius muscle and the thickness of the posterior part of the ligament.

Except in size, the structure of the tympanostapedial syndesmosis in bats closely resembles that in man. Movement of the footplate in the oval window is probably a rocking motion, during which the anterior pole of the footplate is the more active, and the posterior pole remains relatively fixed. In the mole, however, the annular ligament appears to be loose, relative to that of the other forms investigated. This looseness suggests that more of the footplate may be actively involved in movement, and that the movement is more piston-like than in other forms. The anterior pole still seems to be the more active part (in terms of movement) in the mole but the amount of excursion of the central portion and posterior pole is probably greater than in those forms in which the latter areas are relatively fixed by the thicker posterior portion of the ligament and the tension applied to it by the stapedius muscle; this muscle is poorly developed in the mole. This type of motion is even more strongly suggested in other species of Talpidae in which the vestibular surface of the footplate is markedly convex. This feature of the footplate is well marked in the talpid *Mogera and Eoscalops*

(Gaughran, 1954), and also in the rodents *Thomomys* and *Perodipus* (Cockerell, Miller and Printz, 1914). A rocking motion of the footplate in these forms would seemingly be considerably less effective in setting fluids of the inner ear in motion than it would in forms having flat vestibular surfaces of the footplate. This could be interpreted as a protective modification against strong vibratory stimuli, but additional study of the position and direction of movement of the ossicular lever arms in these forms is necessary before this point can be elucidated.

In bats and insectivores the stapedius muscle is invariably multipennate. A cartilaginous or osseous skeletal element of Paauw is present in bats, but is not found in relation to the stapedius in insectivores. This element is considered by de Beer (1937) and Westoll (1945) to represent a part of the extracolumella of reptiles, McGrady (1938) believes it to be a sesamoid bone, as does McClain (1939) from his study of the embryological development of the ossicle in the opposum; this is suggested by its variability in size, and its regularity in appearance and time of ossification, since it forms at least two days after the hyoid arch detaches from the stapes. The latter author further states that, since sesamoid bones are considered to be phylogenetically inherited, it may be that this is the extracolumella functioning as a sesamoid bone. That it functions as a sesamoid bone in the forms considered here is strongly suggested by its characteristic position, just beneath the mucous membrane of the middle ear, in an area where friction involving the membrane and the tendon would occur.

Of particular interest is the tremendous development of the stapedius muscle in two representative *(Eumops* and *Tadarida)* of the Family Molossidae. In *Tadarida* this muscle is approximately eight times larger than is the stapedius muscle in *Glossophaga*, a bat of equal size. It is actually and comparatively larger (generally in the range of three times) than the stapedius muscle in other bats. The inervation of this muscle is rich in all forms, but *Tadarida* (Fig. 37) appears to show an even greater abundance of nerves. Such a rich nerve supply may indicate a large number of small motor units in the muscle, which would be significant in that it would allow for extremely delicate control. The tensor tympani muscle does not appear to be as richly innervated, and probably does not have the potential for the minute control seemingly expressed in the stapedius.

The tensor tympani muscle in most mammals is roughly fusiform in shape, and it inserts by means of a single, cylindrical tendon into

the muscular process on the inner surface of the malleus. In bats, however, the tensor tympani is variably expressed. Based on forms considered in this investigation, and those considered by Wassif (1950), three types of insertions are found among the Chiroptera. The muscle inserts into a muscular crest by a broad tendinous band in some representatives of the Emballonuridae and Molossidae; the muscle shows two tendons of insertion into two muscular tubercles in Rhinopomatidae and Megadermatidae and some of the Hipposideridae, Emballanuridae and Molossidae. In the Pteropidae, Rhinolophidae, Vespertilionidae, Desmodontidae, Natalidae, Furipteridae, Mynopodidae, Mystacinidae, Phyllostomatidae and some Emballonuridae, Hipposideridae and Molossidae, the muscle inserts by a single tendon into a single muscular process. The latter form of insertion is that expressed in most other mammalian forms, including all of the Insectivora considered here, except *Scalopus*, which lacks a tensor tympani muscle.

Although a single tendon inserting into a single muscular process appears to be the usual condition among Mammalia in general, certain evidence suggests that this form is not the primitive type. In *Ornithorhynchus* the muscle consists of two parts, which are inserted into the malleus (Eschweiler, 1911). McClain (1939) reports that during embryonic development the tensor tympani muscle in *Didelphys (Didelphis)* has a double tendon with separate insertions. That the muscle is bipartite in the platypus, and that it is partially divided in the early development of the opposum and later comes to insert by means of a single tendon, supports the suggestion that insertion by a single tendon is not a "primitive" feature. Wassif (1946) thinks that the broad insertion on a muscular crest might be the primitive condition since Doran's (1878) figures and descriptions of the malleus in different species of mammals indicate that the processus muscularis may be found either on the neck of the malleus or lower down on the manubrium, midway between its base and tip. If the processus muscularis extended as a crest between these two points, then the muscle could have been inserted along the broad edge of the crest. Thus, Wassif considers that the broadly-inserted tensor tympani of *Nycteria* approaches this state, and appears to represent a primary condition from which the types of insertion in other bats can be derived. He concludes that different species of bats show stages in the separation of the tensor tympani into two portions, and disappearance of a shorter outer part (head) with corresponding modification in the form

of the muscular process. As noted in this investigation, separation into two tendons of insertion appears to be caused by the chorda tympani nerve, which passes between them. In *Glossophaga* and *Eumops* this nerve passes through the osseous muscular crest rather than splitting the band-like insertion.

The size of both the tensor tympani and stapedius muscles in bats and insectivores is extremely variable. Generally speaking one would expect the size of any given muscle to be dependent on the size of the animal and/or the size of the part of parts upon which it acts; also, functional usage, or frequency of use should govern the morphological magnitude of a muscle. Citing Galambos (1942), Griffin (1958) states that, ". . . these (intra-aural) muscles are enormously large in bats, relative to the size of the animal as a whole." Comparison (Table 2) of the volume of the tensor tympani muscle of *Cryptotis* with that of a bat of approximately equal size (*Natalus*), indicates the validity of this observation, for the muscle in the bat is approximately four times as large as that in the shrew. In addition, *Erinaceus*, although considerably larger than *Eumops*, has a tensor tympani muscle the total volume of which is less than that in *Eumops*. Among Chiroptera, there is considerable variation in the size of both the stapedius and tensor tympani muscles. In the tensor tympani alone, the fiber volume of the muscle and the volume of the tendon show no consistent relationship, and in none of the bats considered are the volumes of the muscles correlated meaningfully with the frequency groupings of the bats. Furthermore, size of the muscles is, obviously, not related to the size of the animal or to size of the parts on which they act. Therefore, their large size must indicate that they are frequently used and of considerable functional importance to the animal.

Although Galambos (1942) comments on some functions of the intra-aural muscles in bats, his observations are primarily directed toward their influence in cochlear responses. According to Griffin (1958:137):

> One possible explanation for the large size of the tensor tympani and stapedius muscles in bats, and the operation of the intra-aural reflex at frequencies up to 55 kc, is that their hearing is very sensitive over this frequency range and requires protection from intense ultrasonic sounds, just as the ears of other mammals do at lower frequencies.

The function of these muscles in most mammals is generally said to be the protection of the inner ear from loud noises; it is said that co-ordinated contractions of these muscles result in decreased senitivity to low frequency sounds of low intensity, and marked

increase in sensitivity toward high frequency, high intensity sounds (Crowe, 1932, Stevens, Davis and Lurie, 1935; Stuhlman, 1950). The importance of a tightly-stretched tympanic membrane and a small, delicately-coupled, ossicular chain has been repeatedly emphasized in discussing factors in the reception and transmission of high frequency and ultrasonic vibrations in forms considered in this investigation. Undoubtedly the intra-aural muscles in bats, as in other mammals, are at least partially responsible for providing these conditions, and, although these muscles may act in some protective manner, it seems probable that the tensor tympani and, especially, the stapedius are of more importance in bats in "tuning" the middle ear for the transmission of ultrasonic vibrations. This finds some support in the work of Galambos (1942), who reports indications that the intra-aural reflex operates throughout the range of sounds emitted by bats.

Griffin (1958:137) also refers to a theory of Hartridge (1945) which, although widely accepted, needs further consideration.

> An alternative theory proposed by Hartridge is that during the act of echolocation a bat's ear requires the same sort of protection as that built into sonar and radar instruments whereby the receiver is temporarily disconnected during the transmission of the intense outgoing signal (183). The essence of this suggestion is the assumption that during the emission of each pulse of high frequency sound a bat's cochlea would be severly taxed by the high intensity of sound coming from the animal's own larynx (either directly through the tissues, or through the air from the mouth around the ear canal), and that the muscles of the middle ear therefore contract just as each pulse is emitted so as to provide the necessary protection.

Griffin considers Hartridge's theory only as a speculative possibility because of the rapidity of the contractions which would be required of the intra-aural muscles, and because of lack of direct evidence concerning the time of contraction of these muscles in the active bat. In serial sections prepared for this investigation the petrosal bone, containing the cochlea, is almost completely isolated from the adjacent bones of the skull; this is especially marked in *Rhinolophus* where all articulations of the petrosal are membranous, and adjacent bones are usually separated, one from another, by pads of fatty or vascular tissue. In addition, the area between the tympanic region and the larynx is extensively invaded by fat and/or glandular tissue. This structural arrangement is incompatible with transmission of high frequency vibrations, either through soft tissues or through bone, regardless of whether the sound emanates from the larynx, or from an external source. These observations tend to support Griffin's (1958) implied rejection of Hartridge's theory.

Since considerable emphasis has been placed on the relative size of structures of the middle ear in reference to frequency transmission, it would seem that the size of the animal would be an important factor governing the size of structures of the middle ear. Griffin (1958:125), from his own observations coupled with those of Schleidt (1951), has suggested a relationship between the size of an animal and the upper frequencies which can be heard.

> Since the rat-sized rodents studied by Schleidt showed response thresholds which rose more steeply in the frequency range from 20 to 40 kc, and since dogs and cats seem to be somewhat more sensitive to high frequencies than men, it seems likely that there is at least an approximate relationship between the size of the mammal and the upper frequency limits of its hearing. The validity of this concept cannot be judged in any throughgoing fashion from the data yet available, but it does seem to be a plausible working hypothesis that the smaller the mammal the shorter the wave lengths of sound to which it can respond. It is of interest in this connection that the smallest of the mice studied by Schleidt weigh 15 to 20 grams, whereas *Myotis lucifugus,* the species of bat used most extensively in our studies, weighs only 6 to 8 grams. Yet we must not overwork this hypothesis and assume that because small mammals such as bats hear better than we do at high frequencies their range of hearing is merely shifted upward. For Galambos' electrophysiological measurements described below show that the bat cochlea may be sensitive to frequencies as low as 30 c. p. s—not far above the lower limits of the human ear. A shift in the upper limit of hearing does not necessarily imply a similar shift in the lower limit.

The evidence gathered in this investigation supports Griffin's idea that there is at least an approximate relationship between the size of the mammal and the upper frequency limit of its hearing. As pointed out above, there is a good correlation of both ossicular volume and size of the tympanic membrane with the upper frequencies utilized in the bat's ultrasonic pulse. Size of the membrane and the ossicles, however, do not always correspond to that which might be expected from the size of the animal. This is especially evident in comparing the relative size of these structures in *Tadarida* and *Glossophaga,* both of which are of approximately the same weight and size. The tympanic membrane of a representative of *Tadarida* is 5.0 sq. mm. in area, while the membrane of a representative of *Glossophaga* has an area of only 2.4 sq. mm. Also, ossicular volume and the volume of intra-aural musculature is considerably greater in *Tadarida* than in *Glossophaga.*

The great variations in size of the auditory ossicles among closely related forms appears to be related to environment. Fossorial mammals, which are assumed to live in a low frequency environment, show middle ear structures which indicate a wide range

of adaptations in the direction of low frequency acuity. In general, there seems to be a tendency toward an increase in ossicular volume, a decrease in the size of the intra-aural muscles, and sometimes, even complete degeneration of the tensor tympani. All of these factors suggest adaptations toward low frequency perception and acuity. The great variations in ossicular morphology reported in the Chrysochloridae (Cooper, 1928), support this view. The Chiroptera, on the other hand, are exceedingly small forms, most of which are essentially blind and highly dependent on their radar-like auditory system. Their small size, aerial environment, and morphology of the middle ear all point to high frequency (ultrasonic) acuity.

Although much emphasis has been placed on morphology of the middle ear, other parts of the auditory system have been modified along lines suggesting adaptations toward high frequency perception. Anyone who has studied bats, even from the standpoint of external form, has undoubtedly been impressed by the elaborate structure of the pinna in many forms. This structure, which presumably funnels sounds toward the tympanic membrane, may be small and "normal" in appearance, or it may be developed to the extent that its length is even greater than that of the animal, as in *Plecotus*. Another peculiar modification is found in the Molossidae, where the pinnae of the two sides are fused across the midline and extend forward over the eyes and beyond the tip of the nose. A structure associated with the pinna which seems to guard the external meatus is the tragus. Griffin (1958) states that the dimensions of the pinna and tragus seem to be of the same order of magnitude as the wave lengths of sounds used by bats for echolocation.

Although the cochlea of the bat is somewhat similar in structure to that of other mammals, certain features of it have apparently evolved to facilitate ultrasonic acuity. The basal whorl of the cochlea, which is concerned with high frequencies, has been found to be unusually large in bats (Iwata, 1924; Ikeda, Yoshindo, and Yokote, 1939). Other modifications of the cochlea involve the structure of the basilar membrane and the position of the round window (fenestra cochleae). According to Griffin (1958:132), "the 'round' window makes contact with the fluid of the inner ear in a quite different position than in other mammals, not at the end of the cochlea but almost a millimeter farther along its first turn." He further states that the basilar membrane is provided with an

additional thickening so that the portion apparently free to vibrate in response to sound is narrower than would otherwise be the case.

Stefanelli (1944a; 1944b) describes different degrees of development of the acoustic and vestibular organs of various species of Microchiroptera in relation to their attitudes of flight, or their flight patterns. Although his studies are concerned with the structure of the ear in relation to flight, he too notes diversity in the degree of development of the three parts of the ear, and finds the same diversity expressed in the auditory portion of the central nervous system. Thus, as he states, it seems that any one of the three parts of the ear, external, middle, or inner, may be proportionately better developed than the others. Adaptations to certain frequencies may favor external, middle, or inner ear specializations, or any combinations of these. In other words, the collecting apparatus may be greatly developed, as in *Plecotus;* the ossicles may show adaptations toward reduction in mass, as is suggested by the structure of

TABLE 1.—Relationships of Some Features (Area of the Tympanic Membrane, Inclination of the Tympanic Membrane From the Horizontal, Area of the Footplate of the Stapes, Ratio of the Area of the Footplate of the Stapes to That of the Tympanic Membrane, Mechanical Advantage Produced by the Ossicular Lever Arms, and the Volume of the Cochlea. Measurements of Area are Expressed in Sq. Mm., Volume in Cu. Mm. and Inclination in Degrees.

GENUS	Tympanic membrane area	Tympanic membrane inclin.	Footplate area	Ratio TM/FP	Ossicular mech. adv.	Cochlear volume
High ultrasonic forms:						
Glossophaga	2.4	70	0.075	32:1	4:1	1.45
Natalus	1.2	60	0.072	16:1	5:1	1.75
Myotis	2.4	45	0.075	32:1	4.3:1	1.45
Rhinolophus	2.5	80	0.150	17:1	4:1	9.20
Cryptotis	1.9	23	0.030	63:1	4:1	0.50
"Intermediate" ultrasonic form:						
Eptesicus	3.0	54	0.063	47:1	3.5:1	2.00
Low ultrasonic forms:						
Tadarida	5.0	50	0.094	53:1	3:1	4.50
Plecotus	6.3	55	0.140	45:1	3.6:1	2.25
Eumops	11.3	50	0.225	51:1	3.3:1	7.75
Nonultrasonic forms:						
Erinaceus	20.5	23	0.400	51:1	4.6:1	5.90
Scalopus	11.3	27	0.780	14:1	2.2:1	2.10

TABLE 2.—Intra-aural Muscle Volumes (Total Volume, and Volume of Muscle Fibers) and Their Relationship to the Size of the Animal, the Size of the Structures (Tympanic Membrane and Ossicles) on Which They Act, and to the Frequency Ranges Utilized by the Various Forms. Volume is Expressed in Cu. Mm. and Area in Sq. Mm.

GENUS	Weight in Grams	Total volume tensor tympanic	Muscle volume tensor tympanic	Stapedius M. volume	Tympanic membrane area	Total ossicular volume
High ultrasonic forms:						
Glossophaga	10.0	0.090	0.048	0.047	2.4	0.046
Natalus	5.5	0.088	0.068	0.047	1.2	0.036
Myotis	8.6	0.099	0.061	0.105	2.4	0.064
Rhinolophus	25.0	0.280	0.162	0.050	2.5	0.059
Cryptotis	5.0	0.020	0.016	0.070	1.9	0.050
"Intermediate" ultrasonic form:						
Eptesicus	20.0	0.131	0.123	0.200	3.0	0.056
Low ultrasonic forms:						
Tadarida	10.0	0.170	0.086	0.380	5.0	0.174
Plecotus	13.4	0.130	0.100	0.126	6.3	0.119
Eumops	55.0	0.900	0.217	0.700	11.5	0.594
Nonultrasonic forms:						
Erinaceus	700	0.764	0.744	0.490	20.5	1.619
Scalopus	80	.....	.....	0.033	11.3	0.588

the stapes in *Glossophaga*, or the inner ear may be tremendously developed, as is certainly the case in *Rhinolophus*.

Nevertheless, the information gathered in this investigation indicates that the middle ear is of extreme importance in ultrasonic perception, much more so than previous investigators seem to have realized. It may be that the inability of some mammals to hear ultrasonic sounds is largely due to inefficient transmission by the middle ear, rather than due to cochlear structure. It is interesting, in this respect, to note that Pumphrey (1950) found, in studying the upper limit of frequency for human hearing, that the upper limit of airborne sound was below 16.5 kc/sec., but that sounds up to 100 kc/sec. could be detected when a crystal was held against the mastoid process or temporal region. He concluded that failure of human beings to hear airborne sounds in the upper range is due to failure of transmission by the middle ear.

SUMMARY AND CONCLUSIONS

A detailed study of the morphology of the middle ear in three genera of insectivores and eight genera of bats was undertaken for the purpose of studying morphological features which may be associated with the ability of certain forms to perceive and utilize sounds in the high frequency and ultrasonic ranges. Previous investigations dealing with the structure of the middle ear have been almost entirely restricted to topographical features of the auditory ossicles and tympanic bone, and to taxonomic implications of these features. The structure of the middle ear in most of the forms included in this investigation has previously been undescribed; in addition to supplementing the findings of previous taxonomic works, descriptions included here may provide a basis for future investigations, not only along taxonomic lines but, also, concerned with hearing mechanisms.

The forms available for this investigation are placed into frequency groups based on their reported, or assumed, sensitivity to various frequencies of sound. The mole, *Scalopus*, is placed in the low frequency group; *Erinaceus* is placed in an intermediate frequency group, and the remaining forms are placed in an ultrasonic group, which is subdivided into high and low ultrasonic categories.

Both insectivores and bats are generally considered relatively primitive mammalian forms. In two of the forms considered here, *Erinaceus* and *Cryptotis*, the middle ear is rather primitive and unspecialized in the general mammalian sense of the word; this primitiveness is suggested by the horizontal position of the tympanic bone and associated tympanic membrane, a wide tympanic notch and extensive pars flaccida, a laminated malleus, the nature of the articular surfaces of the incudomalleolar articulation, the occurrence of a syndesmosis between the neck of the malleus and the long process of the incus, relatively poorly differentiated ossicular ligaments, a fibrous ankylosis of the anterior process to the tympanic bone, and relatively poor development of the intra-aural musculature.

Despite the apparent "primitiveness" of the middle ear in *Cryptotis*, there is some experimental and anatomical evidence that shrews can hear sounds in the high frequency and ultrasonic ranges. Morphological features in the middle ear of bats suggest that modifications from the primitive insectivore pattern favor transmission of ultrasonic vibrations by increasing the total mechanical efficiency of the middle ear. Morphological features of the middle ear of the

mole, on the other hand, suggest modifications and adaptations in a direction suitable to its supposed sensitivity to low frequency vibrations.

The size of the ossicles in a given form show an excellent correlation with the higher frequencies utilized by that form; forms known to utilize high frequencies consistently show smaller ossicles than do forms utilizing low or intermediate frequencies. The same relationships hold true for the size of the tympanic membrane; the smaller the membrane, the higher are the frequencies which the animal seems capable of utilizing. In many bats which utilize high ultrasonics, the ossicles have deep sulci which, in effect, reduce ossicular mass. In addition to being delicate, the articular surfaces of the malleus and incus form acute angles and are capable of being closely coupled so that energy loss through friction in the transfer of vibration from malleus to incus is considerable lessened.

Other morphological features of the middle ear in bats suggest further adaptations along lines of ultrasonic perception. The tympanic membrane tends to assume a more vertical position in bats than in insectivores; in addition, it has a rounded contour and shows a reduction in the size of the pars flaccida. Associated with the annulus fibrosus is a series of vascular channels, the cavernous tissue, which may possibly affect tension of the tympanic membrane. Tension applied to the ossicular complex and tympanic membrane appears to favor transmission of ultrasonic vibrations across the middle ear and possibly "tunes" the system to these frequencies. The amount or degree of tension which can be applied to the tympanic membrane and ossicular chain is dependent upon the degree and force of the contractions of the intra-aural muscles. These muscles are normally considered protective in function, but their high degree of development in bats suggests that they have been modified for additional functions, such as that of tuning. The stapedius muscle, for example, shows a rich innervation in some forms and is, seemingly, capable of delicate control of the ossicular chain. The large size of the intra-aural muscles, and the tensions that they apply to the ossicular complex, appear to account partially for the discrete, well-developed ligaments that anchor and suspend the ossicular chain.

The structures of the middle ear in the mole show adaptations essentially opposite in character to those noted in bats. The tympanic membrane is large in proportion to the size of the animal, and it has extensive attachments to the malleus. The ossicles are

rather massive, are somewhat loosely articulated and have relatively flat articular surfaces; the stapedius muscle is poorly developed and the tensor tympani is wanting. These features appear to be adaptations to low frequency transmission.

The notable differences in the structure of the middle ear between that of the supposed primitive state and that seen in bats and the mole, all suggest that the size of the tympanic membrane, the size of the ossicles, the morphology of the incudomalleolar articulation, and the structure of the intra-aural muscles are of major significance to the degree of efficiency with which vibratory energy can be transferred from the external ear to the inner ear. While a small delicate middle ear is seemingly necessary for ultrasonic perception in bats, it is not suggested that this is the only means by which it can be accomplished.

Since small size of the structures of the middle ear can be correlated with high frequency and ultrasonic perception, it seems reasonable to assume that other small mammals may perceive, and perhaps utilize, ultrasounds; this has been suggested by other authors who have noted that mannerisms in many small mammals suggest sensitivity of these forms to high frequency sounds. The apparent inability of large terrestrial mammals to hear high frequency sounds possibly is more the result of inefficient mechanisms for the transfer of vibratory energy across the middle ear than it is of the nature of the inner ear itself.

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KEY TO ABBREVIATIONS

AC—anterior crus of stapes
AG—arterial groove
AL—anterior leg of tympanic bone
B—brain
BI—body of incus
BT—bulla tympanica
C—cochlea
CB—central buttress of anterior process
CC—capitular crest
CRS—crural sulcus
CS—capitular spine
CST—crista stapedis
CT—crista tympanica
FCT—foramen for chorda tympani nerve
FP—footplate of stapes
GCT—groove for chorda tympani nerve
HDM—head of malleus
HDS—head of stapes
IAF—inferior articular facet of malleus
IAS—articular surface of incus
IL—inner lamella
ILS—interlamellar sulcus
Lam—lamina
ICIL—lateral component of posterior incudal ligament
LP—lateral process
LPI—long process of incus
LPR—lenticular process
LSC—lateral semicircular canal
MCIL—medial component of posterior incudal ligament
MN—manubrium
MNB—manubrial base
MNS—manubrial spatulation
NM—neck of malleus
OA—orbicular apophysis
OL—outer lamella
PLD—pedicle of lenticular process
PC—posterior crus of stapes
PIL—posterior incudal ligament
PL—posterior leg of tympanic bone
PMS—muscular process for stapedius muscle
PMTT—muscular process for tensor tympani muscle
PPA—pars processus anterioris of anterior process
PS—styliform process of tympanic bone
RM—recessus meatus acustica externi
SAO—shoulder of anterior orus
SAF—superior articular facet of malleus
SIN—sulcus incudis
SL—stapedial labrum
SN—sulcus malleolaris
SPI—short process of incus
ST—sulcus tympanicus
STA—spina tympanica anterior
STM—stapedius muscle
STP—spina tympanica posterior
TL—tubercle for lateral malleolar ligament
V—vein

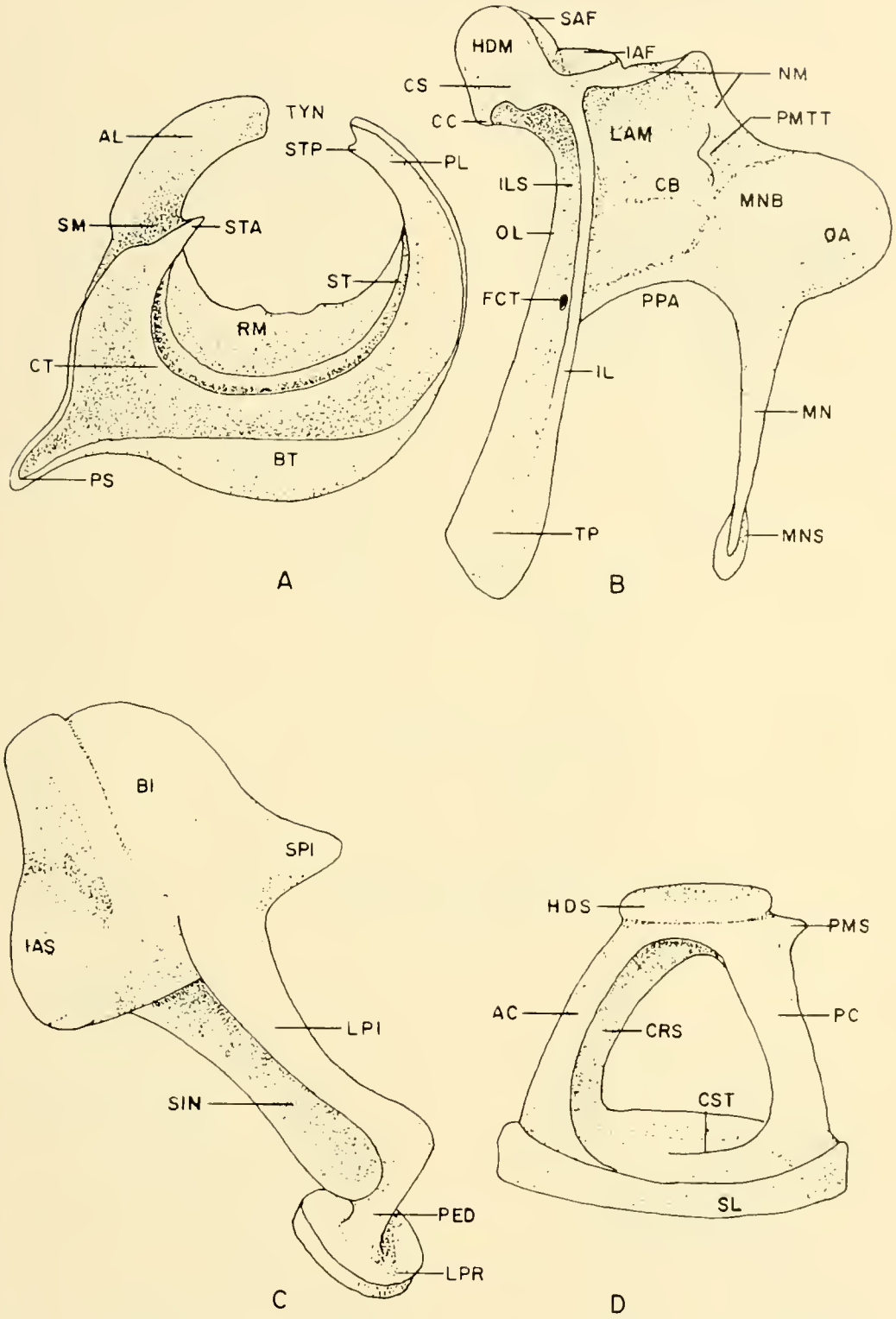


FIG. 1.—Composite diagram showing parts of the tympanic bone (*a*), malleus (*b*), incus (*c*) and stapes (*d*).

THE AUDITORY OSSICLES OF ERINACEUS EUROPAEUS

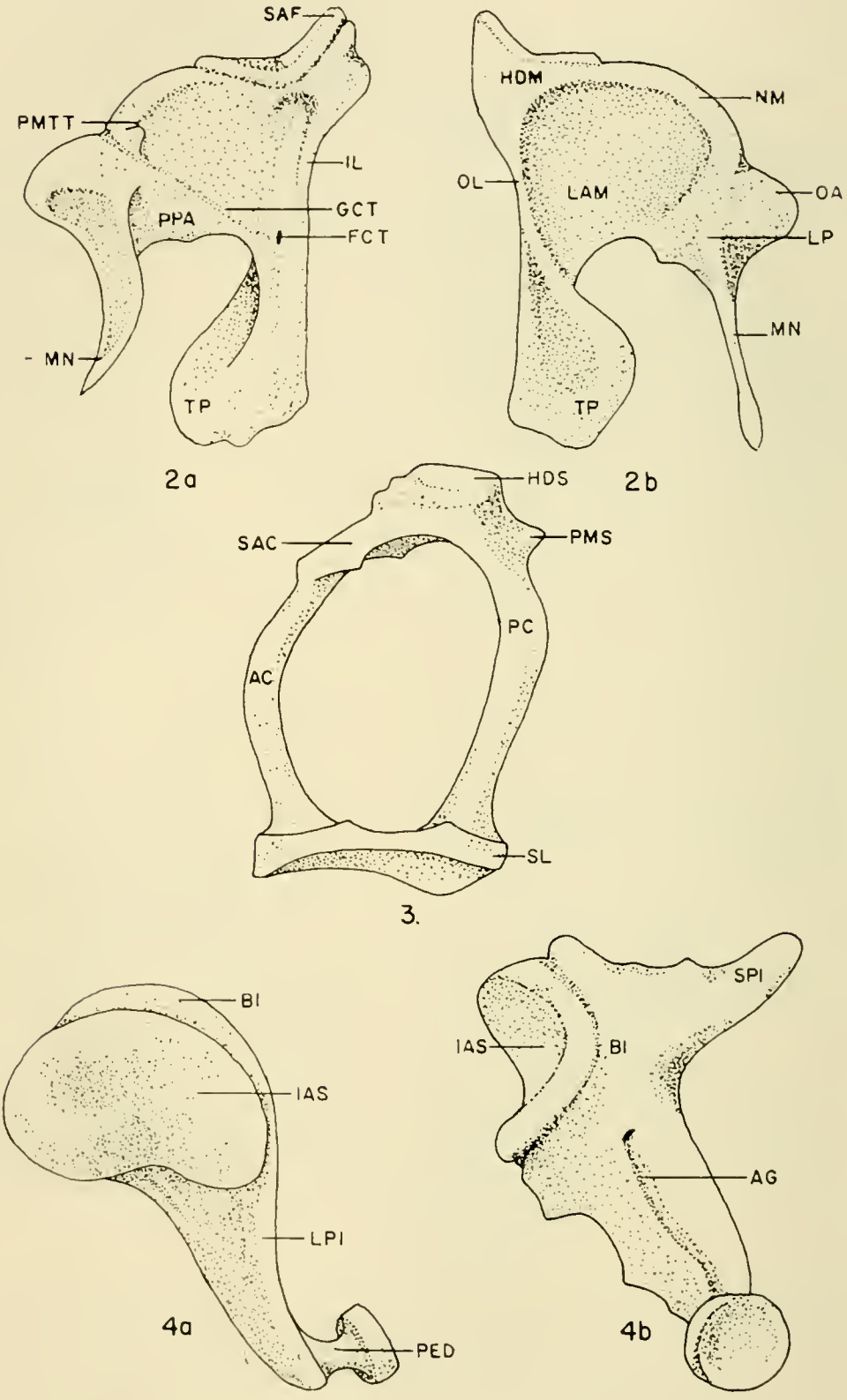


FIG. 2.—Malleus. *a*—external view; *b*—internal view. 10 ×.
FIG. 3.—Stapes. 30 ×.
FIG. 4.—Incus. *a*—ventral view; *b*—medial view. 30 ×.

THE AUDITORY OSSICLES OF CRYPTOTIS PARVA

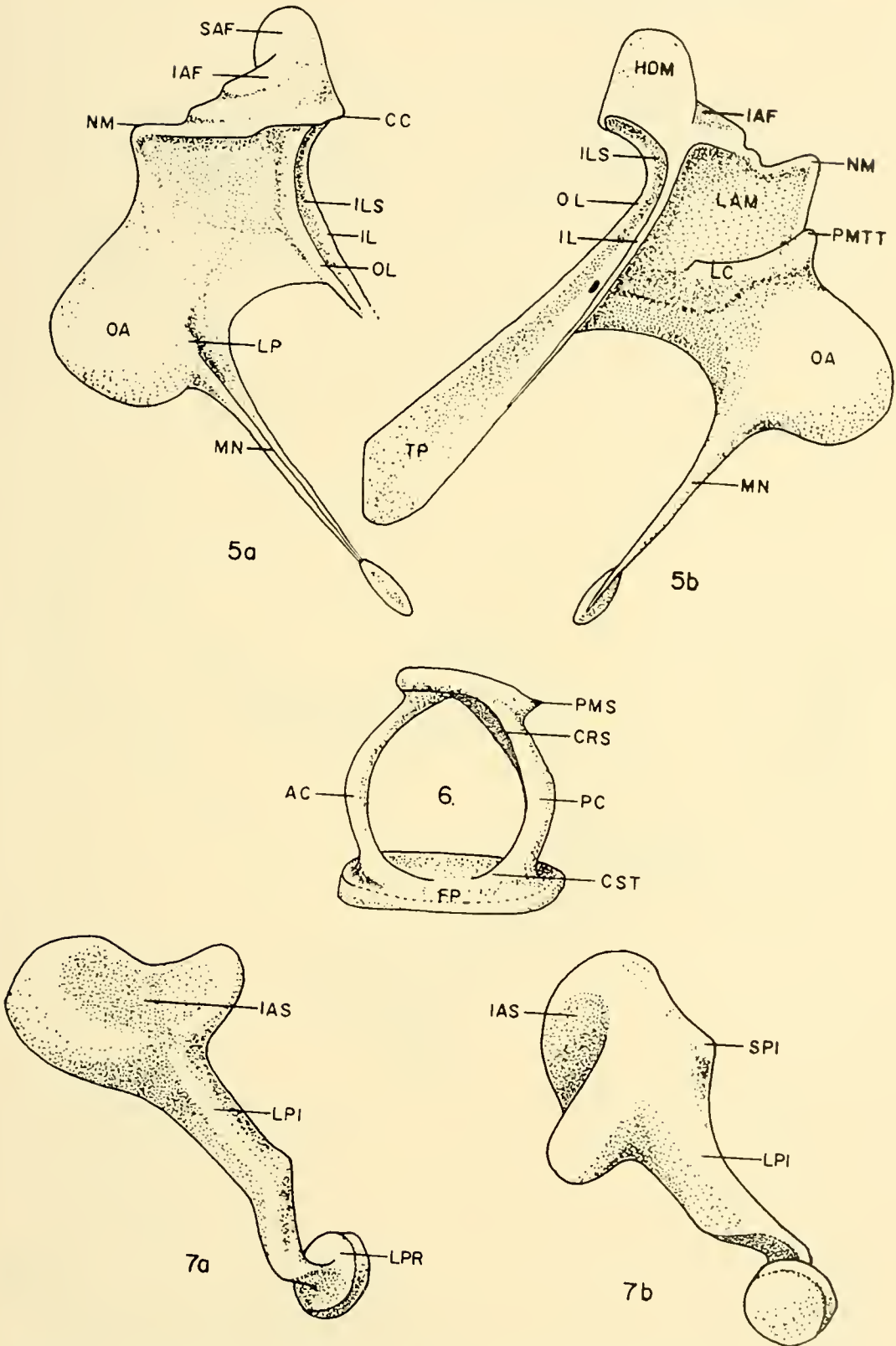


FIG. 5.—Malleus. *a*—external view; *b*—internal view. 25 ×.
FIG. 6.—Stapes. 85 ×.
FIG. 7 —Incus. *a*—ventral view; *b*—medial view. 85 ×.

THE AUDITORY OSSICLES OF SCALOPUS AQUATICUS

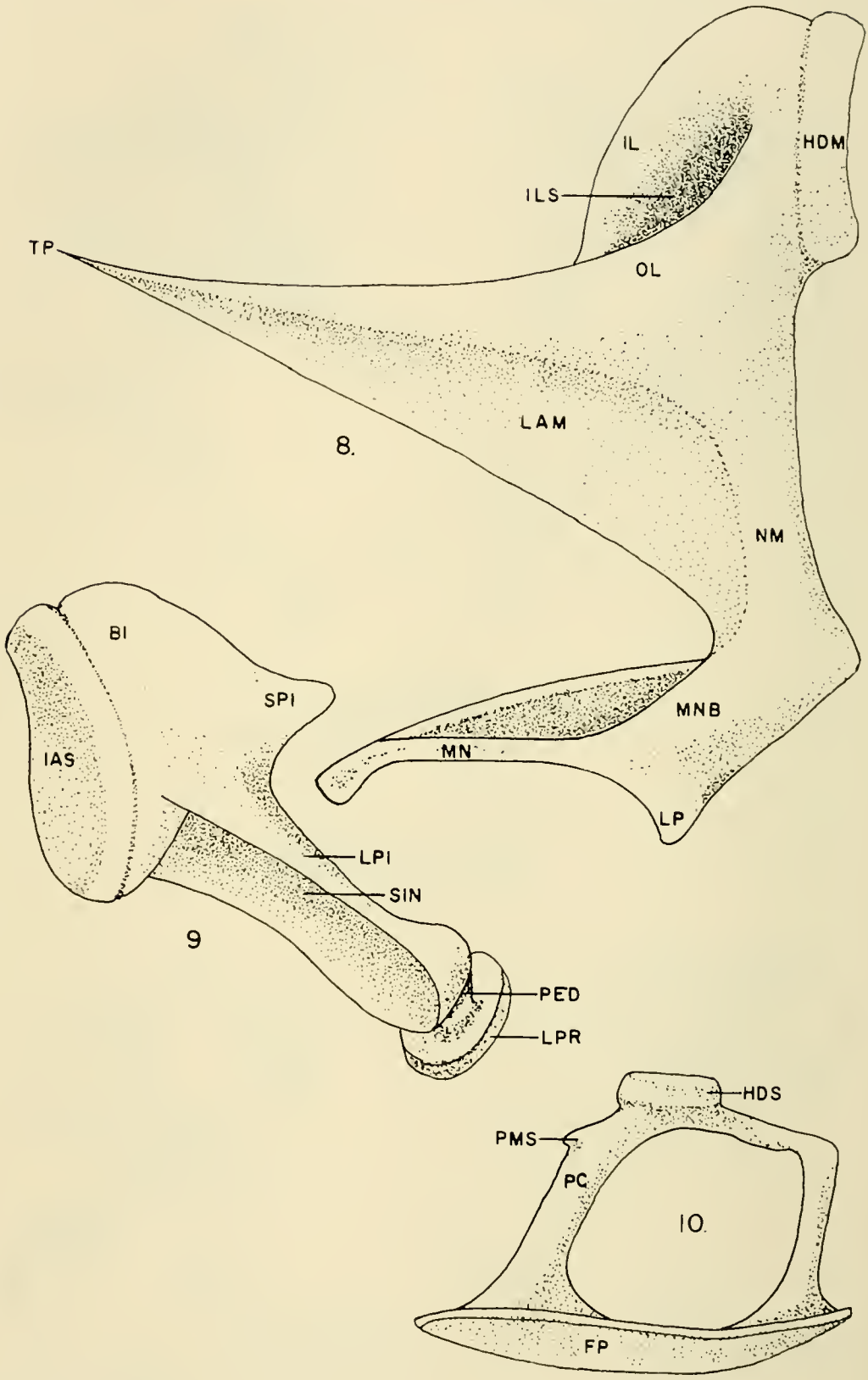


FIG. 8.—Malleus, external view. 30 ×.
FIG. 9.—Incus, external view. 30×.
FIG. 10.—Stapes. 30 ×.

THE AUDITORY OSSICLES OF GLOSSOPHAGA SORICINA

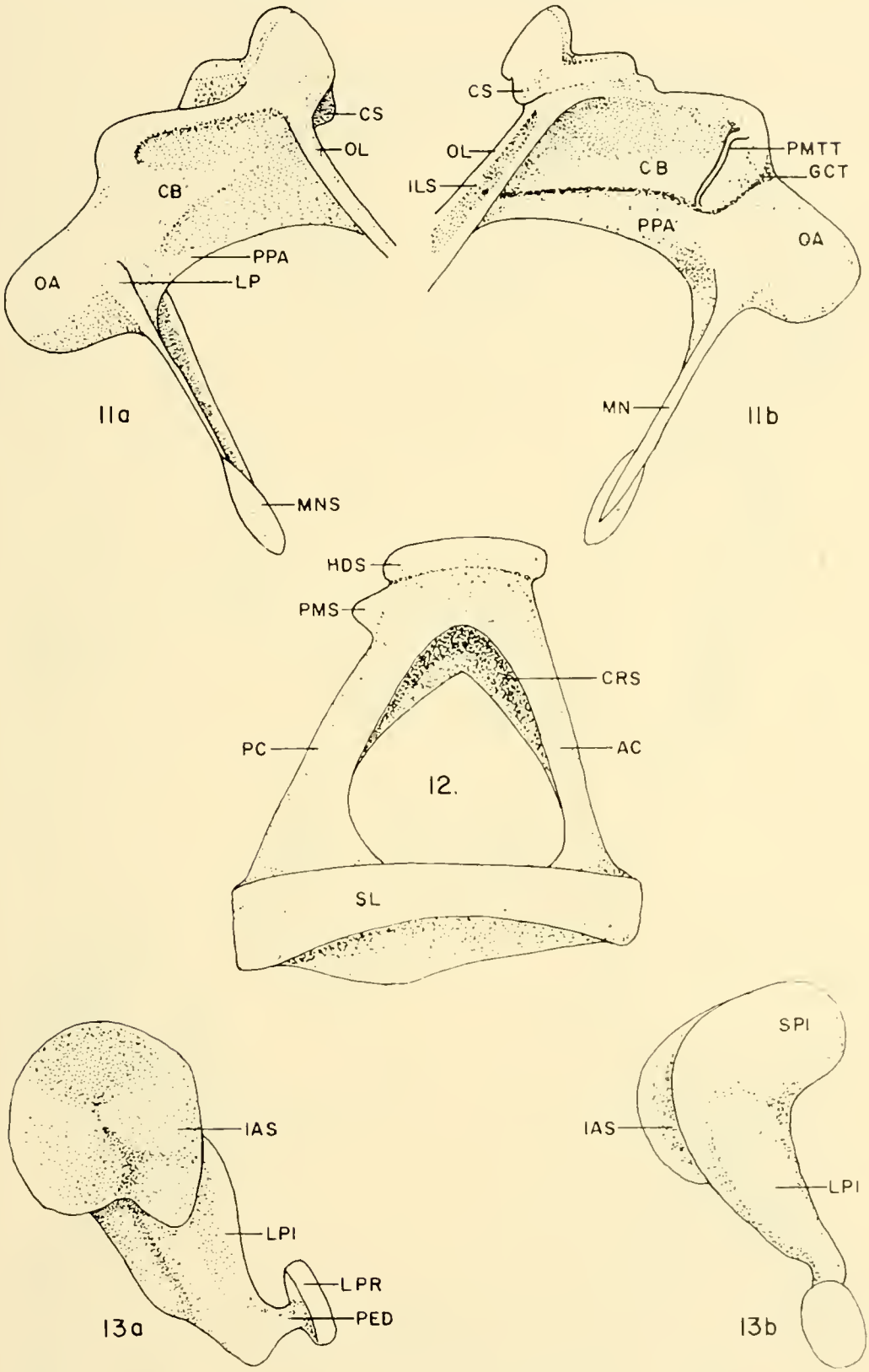


FIG. 11.—Malleus. *a*—external view; *b*—internal view. 40 ×.
FIG. 12.—Stapes. 85 ×.
FIG. 13.—Incus. *a*—ventral view; *b*—medial view. 55 ×.

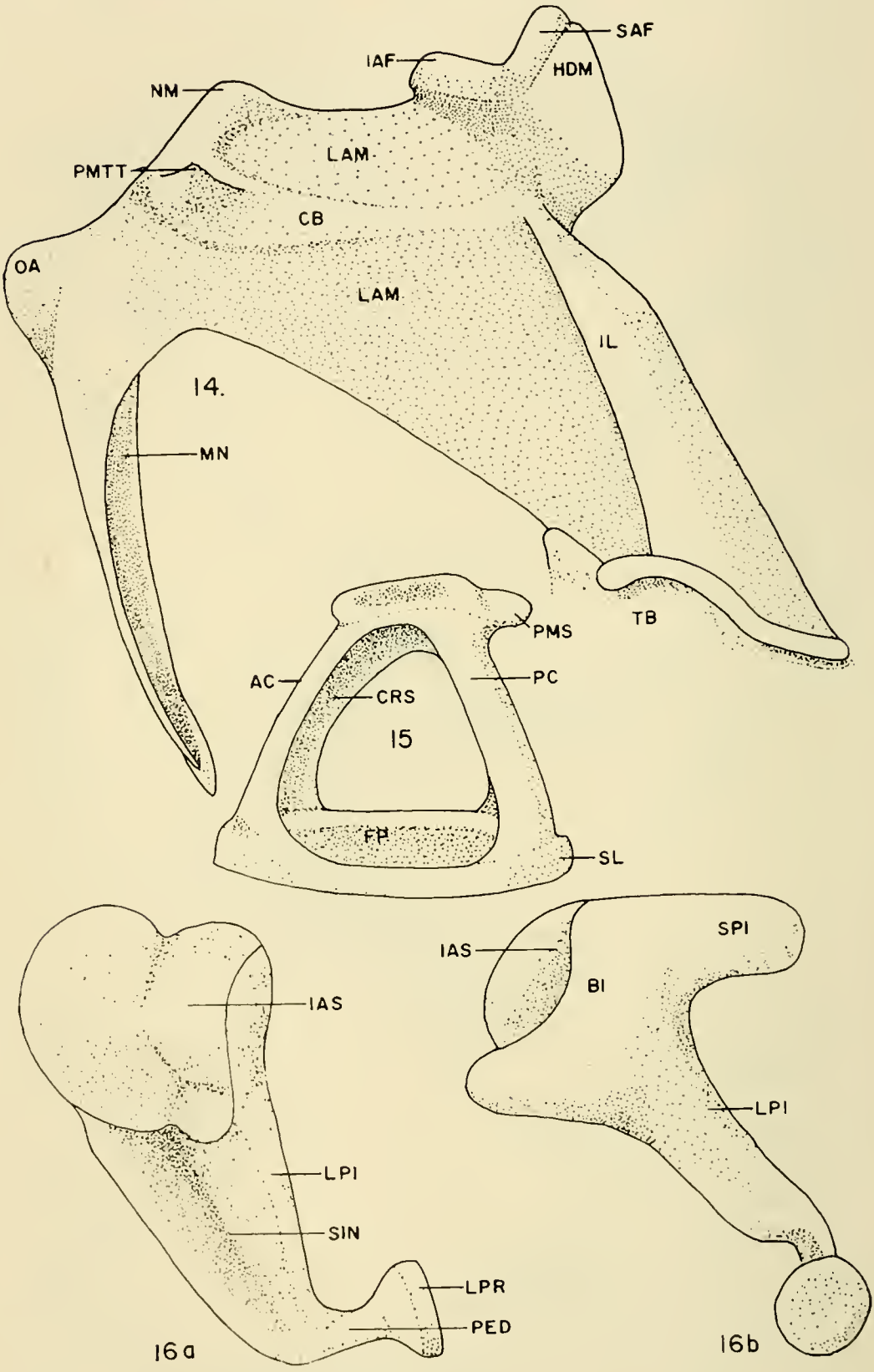


FIG. 14.—Malleus, internal view. 85 ×.
FIG. 15.—Stapes. 130 ×.
FIG. 16.—Incus. *a*—ventral view; *b*—medial view. 130 ×.

THE AUDITORY OSSICLES OF EPTESICUS FUSCUS

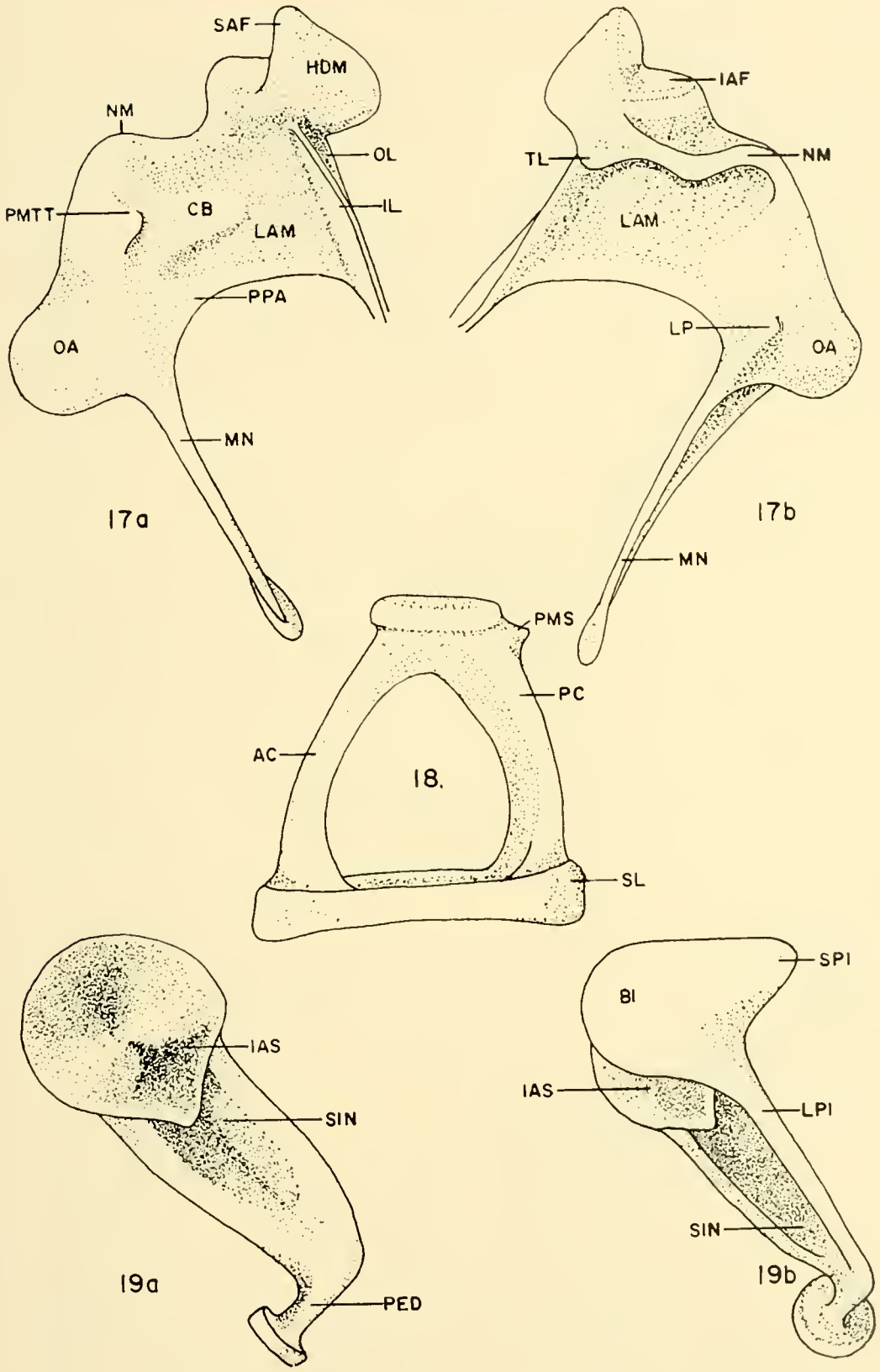


FIG. 17.—Malleus. *a*—internal view; *b*—external view. 40 ×.
FIG. 18.—Stapes. 85 ×.
FIG. 19.—Incus. *a*—ventral view; *b*—lateral view. 65 ×.

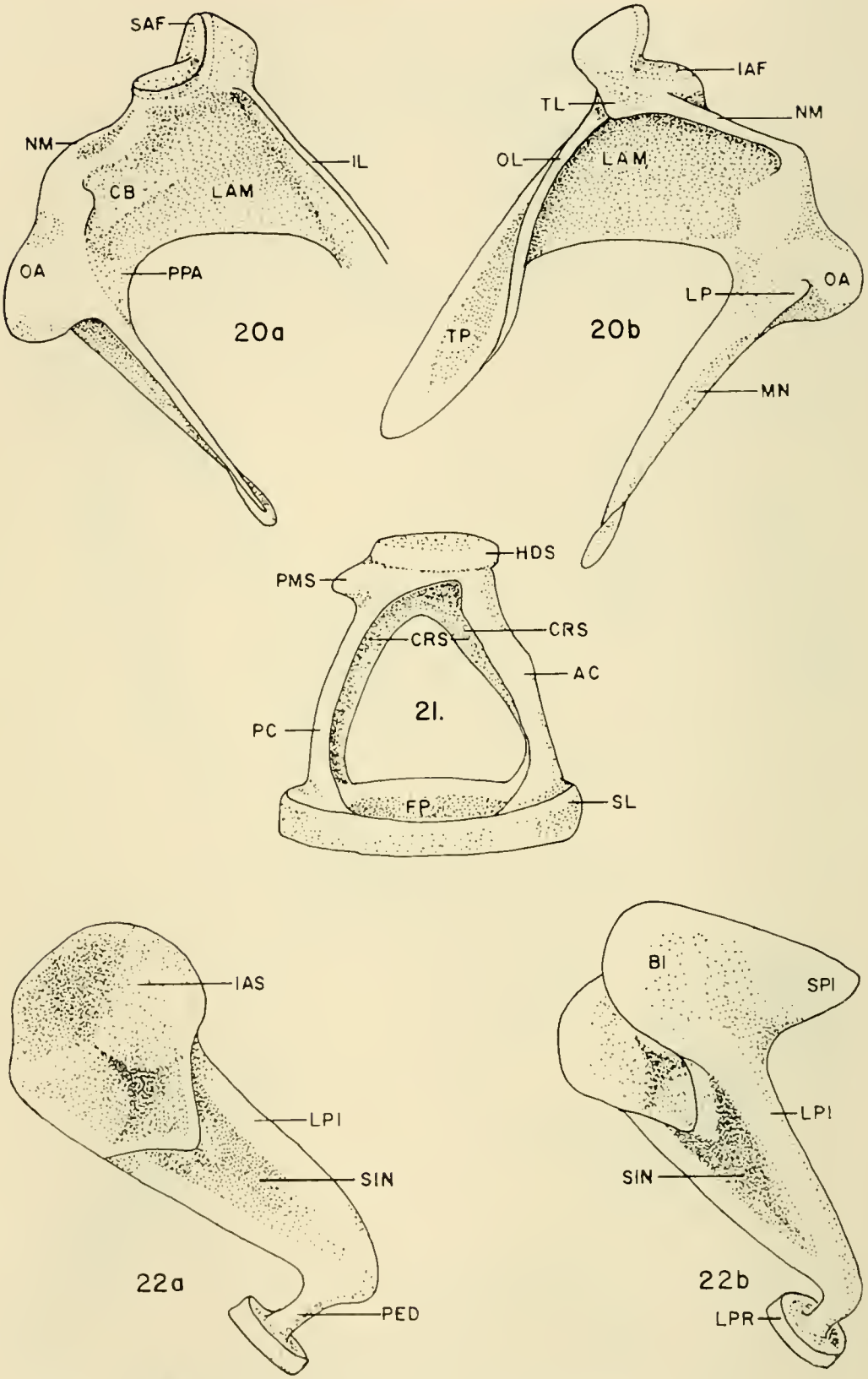


FIG. 20.—Malleus. *a*—internal view; *b*—external view. 40 ×.
FIG. 21.—Stapes. 85 ×.
FIG. 22.—Incus. *a*—ventral view; *b*—lateral view. 85 ×.

THE AUDITORY OSSICLES OF PLECOTUS TOWNSENDII

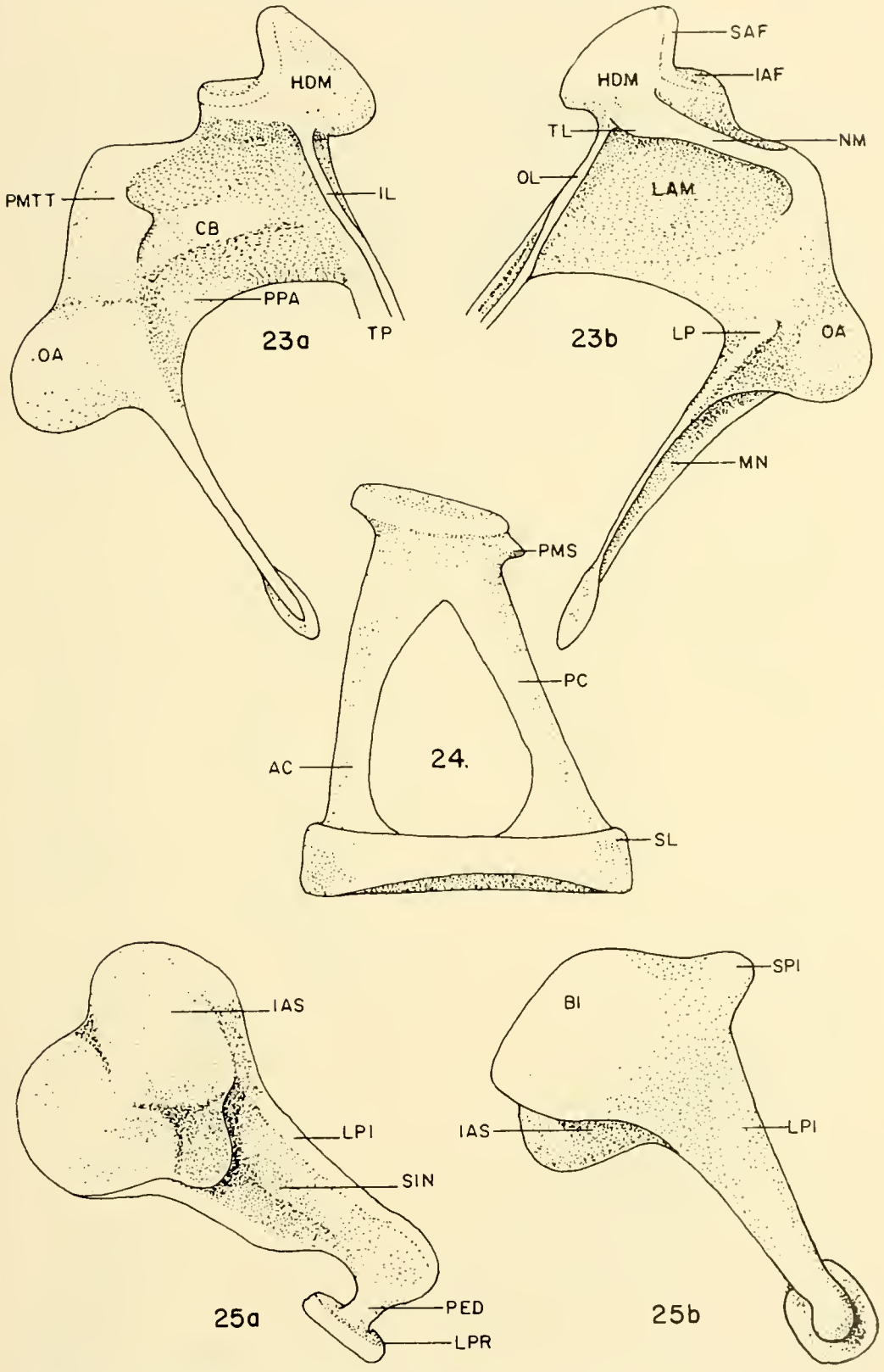


FIG. 23.—Malleus. *a*—internal view; *b*—external view. 35 ×.
FIG. 24.—Stapes. 85 ×.
FIG. 25.—Incus. *a*—ventral view; *b*—lateral view. 60 ×.

THE AUDITORY OSSICLES OF TADARIDA BRASILIENSIS

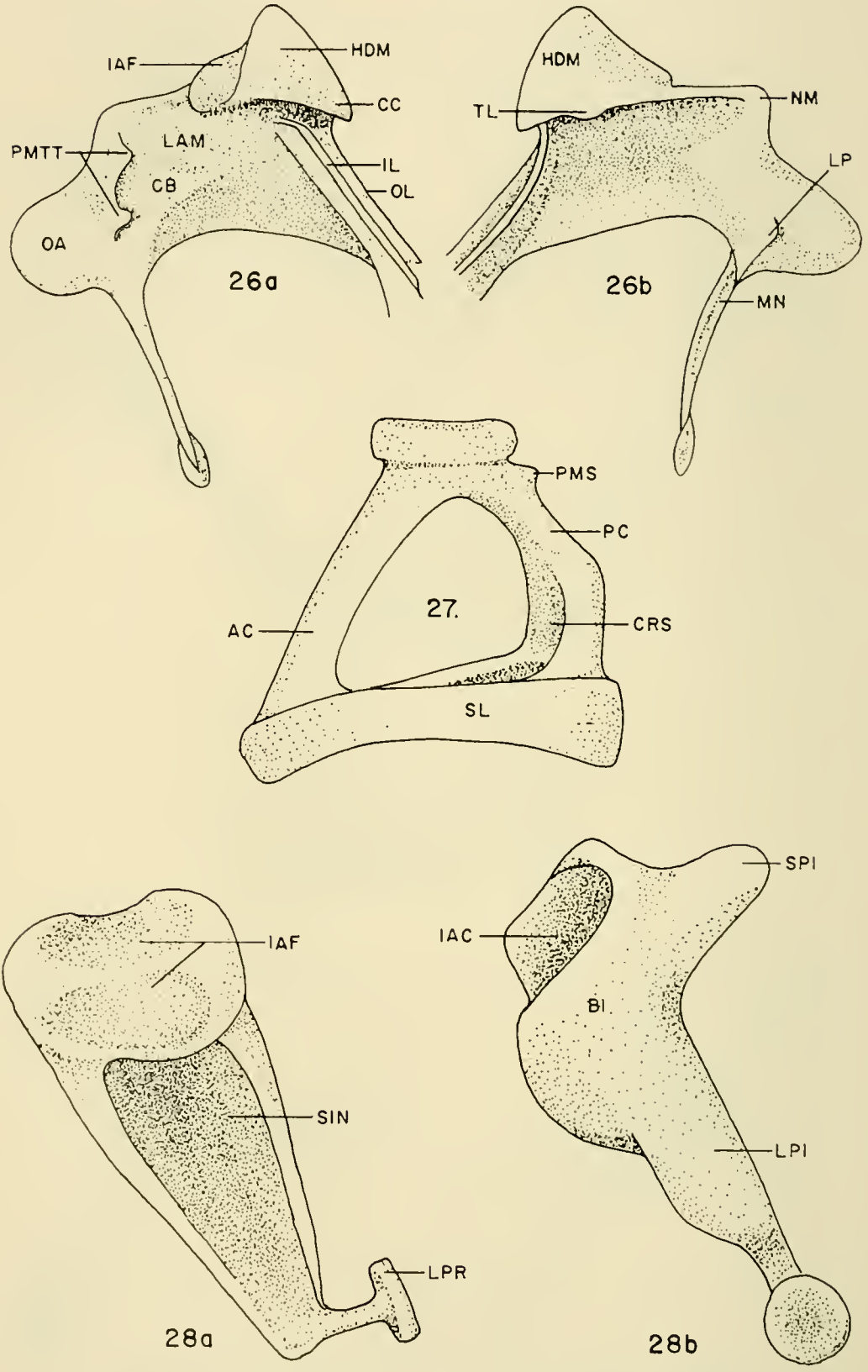


FIG. 26.—Malleus. *a*—internal view; *b*—external view. 27 ×.
FIG. 27.—Stapes. 80 ×.
FIG. 28.—Incus. *a*—ventral view; *b*—medial view. 60 ×.

THE AUDITORY OSSICLES OF EUMOPS PEROTIS

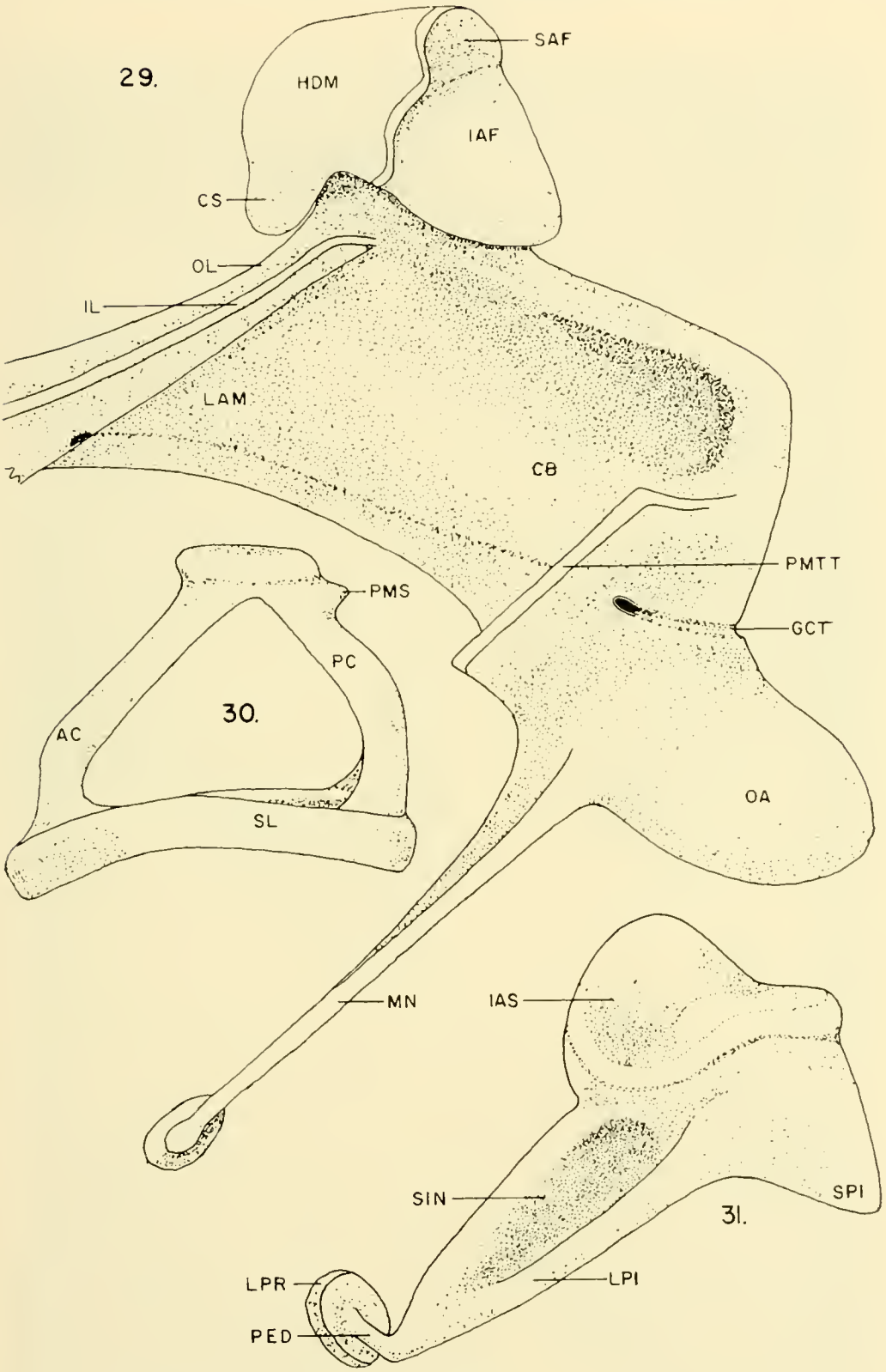


FIG. 29.—Malleus, internal view. 45 ×.
FIG. 30.—Stapes. 45 ×.
FIG. 31.—Incus, lateral view. 45 ×.

FIG. 32.—Transverse section through the posterior incudal ligament of *Erinaceus europaeus.* 47 ×.

FIG. 33.—Transverse section through the posterior incudal ligament of *Crytotis parva.* 130 ×.

FIG. 34.—Transverse section through the posterior incudal ligament of *Scalopus aquaticus.* 93 ×.

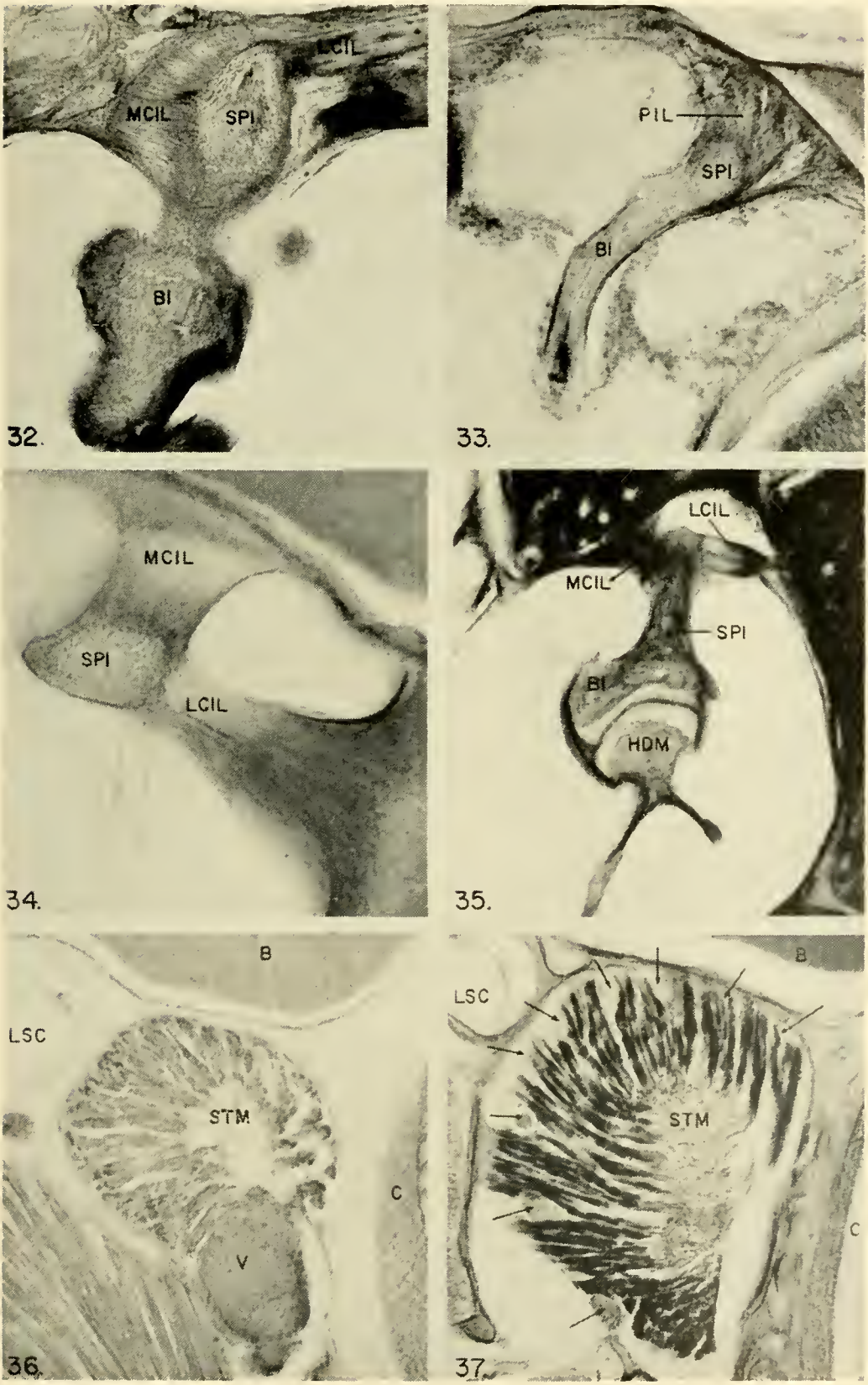
FIG. 35.—Transverse section through the posterior incudal ligament of *Tadarida brasiliensis.* 53 ×.

FIG. 36.—Transverse section through the stapedius muscle of *Natalus mexicanus.* Note that no nerve fibers are visible at a magnification of 95 diameters.

FIG. 37.—Section through the stapedius muscle of *Tadarida brasiliensis.* Note abundant innervation (indicated by arrows). 65 ×.

THE POSTERIOR INCUDAL LIGAMENT AND INNERVATION OF THE STAPEDIUS MUSCLE

Muscle in Chiroptera



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Some New Species of *Rhagovelia* from the Philippines (Veliidae, Heteroptera) *

BY

HERBERT B. HUNGERFORD AND RYUICHI MATSUDA

In preparing a report upon the aquatic and semiaquatic Hemiptera taken by the Chicago Natural History Museum during their Philippine Zoological Expedition (1946-'47), we have found so many new species of *Rhagovelia* that we are submitting this as a separate report. Until now the following five species have been described from the Philippines: *Rh. minuta* Lundblad (1936), *Rh. philippina* Lundblad (1936), *Rh. orientalis* Lundblad (1937), *Rh. luzonica* Lundblad (1937) and *Rh. teretis* Drake (1948). With Dr. Lundblad's splendid paper "Die altweltlichen Arten der Veliidengattungen *Rhagovelia* und *Tetraripis*" (Arkiv för Zoologi, Band 28A, No. 21, 1936) in which he illustrated all species and gave keys to all species for both sexes, and his "Einige neue oder wenig bekannte Ostasiatische *Rhagovelia* Arten" (Entomologisk Tidskrift, Häft 1-2, 1937), also well illustrated, we thought the task of identifying the philippine *Rhagovelia* would be an easy one. To our disappointment, all eight species are new. In describing them we are mindful of the variations in color and structures in the species of *Rhagovelia* from all over the World. Three of them belong to the subgenus *Neorhagovelia* Matsuda not before recorded from the Philippines.

Rhagovelia (Rhagovelia) lundbladi n. sp.

(Fig. 2, a to f)

Size	*Length of body*	*Width of head*	*Width of thorax*
Apterous male	4.2 mm.	0.8 mm.	1.36 mm.
Apterous female	4.3 mm.	0.84 mm.	1.47 mm.
Macropterous female	4.8 mm.	0.84 mm.	1.86 mm.

Color. Apterous forms: Head, metanotum, abdominal tergites, inner third and outer margin of connexivum dark brown. Anterior

* Contribution No. 1078 from the Department of Entomology, University of Kansas. This paper is a by-product of a project supported by a grant from the National Science Foundation.

lobe of pronotum yellowish; anterior half of posterior lobe of pronotum yellowish; anterior half of posterior lobe of pronotum dark brown with a pale median longitudinal line, posterior half brown to yellowish brown. Venter brown to yellowish brown. Underside of first antennal segment, underside of femur and tibia of all legs, coxae and trochanters, acetabula, dorsal base of hind femur, underside of connexivum, and a median stripe on dorsal side of connexivum yellow to yellowish brown. Last three antennal segments and dorsal side of legs dark brown. *Macropterous forms:* Pronotum with more brown pits, hemelytra with black veins and brown membrane.

Structural characteristics.

Male antennal formula: 1st: 2nd: 3rd: 4th:: 50: 25.5: 32: 31.

Female antennal formula: 1st: 2nd: 3rd: 4th:: 45: 26: 31.5: 27.

Male leg formulae	*Femur*	*Tibia*	*Tarsus*
Front leg	60	62	21(1 + 2 + 3)
Middle leg	98	78	5: 27: 42
Hind leg	98	85	10(1 + 2): 20
Female leg formulae			
Front leg	56	58	18(1 + 2 + 3)
Middle leg	90	69	5: 25: 39
Hind leg	87	89	10(1 + 2): 20

Pronotum much longer than an aye, rounded behind, exposing metanotum on sides and behind its rear margin. *Apterous male:* Anterior trochanter unarmed but somewhat hairy. Front tibia hairy, as broad distally as femur, with a longitudinal comb-like ridge on inner surface near distal end. Hind trochanter armed with a number of short pegs. Hind femur incrassate and hairy, armed with pegs as shown on Fig. 2, b, c. Hind tibia curved as shown on Fig. 2, b. First genital segment shorter than last abdominal tergite. Parameres symmetrical, and as shown on Fig. 2, d. *Apterous female:* Hind femur slightly incrassate and armed as shown on Fig. 2, e. Connexivum erect beyond third abdominal segment and somewhat overlapping seventh abdominal tergite, which is more than twice as long as its basal width.

Comparative notes. The shape of parameres are closest to that of *Rh. maculata* Distant from Nigeria, but *Rh. maculata* is black and the armature of the hind femur is entirely different from that of *Rh. lundbladi.*

Data on types: Described from apterous male holotype, allotype and paratypes (6 ♂ ♂, 3 ♀ ♀), and one macropterous female morphotype, all bearing labels "C. N. H. M. Philippine Zool. Exped.

(1946-47) H. Hoogstraal leg.," "E. slope, Mt. McKinley, Davao Province, Mindanao 46," "Stream through original forest" and "Elevation 3000 ft."; three apterous males (paratypes) labelled "Mainit, E. slope, Mt. Apo, Davao Province, Mindanao, 4300 ft. XI, 46," and "Stream through original forest."

Holotype, allotype, female morphotype and some paratypes are in the Chicago Natural History Museum. Other paratypes are in the Francis Huntington Snow Museum, University of Kansas.

Rhagovelia (Rhagovelia) cotabatoensis n. sp.

(Fig. 3, a to f)

Size	*Length of body*	*Width of head*	*Width of thorax*
Apterous male	3.15 mm.	0.735 mm.	1.09 mm.
Apterous female	3.57 mm.	0.714 mm.	1.26 mm.

Color. Body black with gray overcast and scattered golden hairs. Anterior lobe and sometimes posterior margin of pronotum yellow to reddish yellow. Lateral half of connexivum including margin brown. Antennae and legs black except basal half of first antennal segment, all coxae, trochanters, basal half of front femora and basal fourth of hind femora which are pale yellow. Propleura and underside of connexivum pale yellow. V-shaped spot on venter of mesosternum, all of metasternum and abdominal venter except last segment usually dark brown to nearly black with gray overcast.

Structural characteristics.

Male antennal formula: 1st: 2nd: 3rd: 4th:: 35: 18: 22: 22.

Female antennal formula: 1st: 2nd: 3rd: 4th:: 35: 20: 22: 20.

Male leg formulae	*Femur*	*Tibia*	*Tarsus*
Front leg	44	46	13(1 + 2 + 3)
Middle leg	75	54	4: 18: 31
Hind leg	68	57	5(1 + 2): 15
Female leg formulae			
Front leg	43	44	13(1 + 2 + 3)
Middle leg	72	55	3: 20: 32
Hind leg	63	59	5(1 + 2): 15

Pronotum much longer than an eye, rounded behind exposing metanotum on sides and behind its rear margin. *Apterous male:* Anterior trochanter unarmed but hairy. Front tibia hairy, as broad distally as diameter of femur, with the usual longitudinal black ridge on inner surface near distal end. Hind trochanter armed with some pegs. Hind femur only moderately incrassate and armed, as shown on Fig. 3, b, c. Parameres slender, as shown on Fig. 3, d. *Apterous female:* Hind trochanter with one or more

pegs. Hind femur nearly as incrassate as in male, but its armature is different (Fig. 3, e). Connexivum narrow, obliquely erect in first four segments, then constricted and nearly vertically erect to overlap last two abdominal tergites and with a dense mass of hairs at apex. Seventh abdominal tergite more than twice as long as its width (Fig. 3, f).

Comparative notes: This species is near *Rh. lundbladi,* but smaller. The hind tibia of the male is straight, not curved as in *Rh. lundbladi* and the parameres are more slender. This species appears gray while *Rh. lundbladi* is brown.

Data on types: Described from apterous male holotype, apterous allotype and eight apterous paratypes (4 ♂ ♂, 4 ♀ ♀). All bear the following labels: "C. N. H. M. Philippine Zool. Exped. (1946-47) H. Hoogstraal," "Conel Buayan, Cotabato Province, Mindanao 100 ft. XII, 46," "Stream through grassland." Holotype, allotype and some paratypes are in the Chicago Natural History Museum, and some paratypes are in the Francis Huntington Snow Museum, University of Kansas.

Rhagovelia (Rhagovelia) hoberlandti n. sp.

(Fig. 2, g to l)

Size	*Length of body*	*Width of head*	*Width of thorax*
Apterous male	3.57 mm.	0.735 mm.	1.26 mm.
Apterous female	3.53 mm.	0.735 mm.	1.26 mm.

Color. Brown to nearly black above except anterior lobe and rear margin of pronotum and outer half of connexivum which are yellow. Sides and venter brown to nearly black with a gray frosty covering except propleura and ventral margin of connexivum which are yellow. Antennae and dorsal surface of legs dark brown. Basal half of first antennal segment yellow above and almost entirely pale yellow below. Basal half of front femur above and nearly all its venter yellow. Middle femur with a longitudinal yellowish stripe beneath. Hind femur at base dorsally and nearly all its venter pale yellow. All trochanters, coxae and distal ends of acetabula pale yellow. Venter of last abdominal segment in both sexes light brown to nearly yellow.

Structural characteristics.

Male antennal formula: 1st: 2nd: 3rd: 4th:: 41: 21: 25: 24.

Female antennal formula: 1st: 2nd: 3rd: 4th:: 37: 20: 22: 21.

Male leg formulae	*Femur*	*Tibia*	*Tarsus*
Front leg	45	53	16(1 + 2 + 3)
Middle leg	80	61	5: 23: 34
Hind leg	88	76	10(1 + 2): 18

Female leg formulae			
Front leg	44	53	14(1 + 2 + 3)
Middle leg	70	50	4: 18: 34
Hind leg	60	63	9(1 + 2): 13

Pronotum much longer than an eye, rounded behind exposing metanotum on sides and behind its rear margin. *Apterous male:* Anterior trochanter hairy. Distal end of hairy tibia about as wide as diameter of femur, with a longitudinal comb-shaped ridge on inner distal edge (one seventh of the length of tibia). Hind trochanter with one or two large pegs and several smaller ones. Hind femur incrassate, armed with pegs or spinous pegs as shown on Fig. 2, h, i. Underside of femur hairy. Hind tibia thickened near base of distal third and armed with two rows of stouter pegs; distal end of tibia with two stout pointed spines as shown on Fig. 2, h. Last abdominal tergite shorter than two preceding tergites and its caudal end plainly broader than its base. Venter of first two abdominal segments carinate. Venter of last abdominal segment covered with golden hairs, distal third with a median hairy elevation and a depressed area on either side. First genital segment hairy, very short ventrally, and dorsally not as long as last abdominal segment. Parameres as shown on Fig. 2, j. *Apterous female:* Connexivum broad, obliquely raised, outer half of each segment nearly vertical beyond third segment; marginal tufts of long hairs on the margin of fourth and sixth connexival segments; only sixth and seventh abdominal tergites a little longer than their basal widths. Distal half of eighth abdominal tergite slightly elevated and hairy. Venter of seventh abdominal segment longer than preceding segment. Hind femur as shown on Fig. 2, l.

Comparative notes. This species, like *Rh. lundbladi,* is dark brown in color but smaller in size. The last abdominal tergite of the female is relatively shorter and broader than in *Rh. lundbladi.* The shape of parameres will separate this species from *Rh. lundbladi* (see Fig. 2, d and j).

Data on types. This species has been described from the male holotype, female allotype and four paratypes (2 ♂ ♂, 2 ♀ ♀), all apterous and bear the following labels: "C. N. H. M. Philippine Zool. Exped. (1946-47) H. Hoogstraal leg.," "Dimaniang Busuanga Is. P. I. (Calamianes group) nr. sea level III. 47" and "small pool beside stream." Holotype, allotype and two paratypes are in the Chicago Natural History Museum. Two paratypes are in the Francis Huntington Snow Museum, University of Kansas.

Rhagovelia (Rhagovelia) usingeri n. sp.

(Fig. 3, g to l)

Size	*Length of body*	*Width of head*	*Width of thorax*
Apterous male	3.57 mm.	0.756 mm.	1.26 mm.
Apterous female	3.36 mm.	0.756 mm.	1.26 mm.
Macropterous male	4.20 mm.	0.756 mm.	1.65 mm.
Macropterous female	3.99 mm.	0.796 mm.	1.47 mm.

Color. Body black with a faint gray overcast dorsally, except anterior lobe of pronotum and margins of connexivum yellowish to reddish yellow. Thoracic pleura and abdominal venter black with a gray overcast. Basal half of first antennal segment, coxae, trochanters of all legs, basal half of front femur, and base of hind femur yellow. Hemelytra dark brown to black, with a basal longitudinal white band reaching beyond caudal end of pronotum.

Structural characteristics.

Male antennal formula: 1st: 2nd: 3rd: 4th:: 42: 26: 27: 26.

Female antennal formula: 1st: 2nd: 3rd: 4th:: 42: 25: 27: 25.

Male leg formulae	*Femur*	*Tibia*	*Tarsus*
Front leg	50	57	16(1 + 2 + 3)
Middle leg	79	67	4: 21: 37
Hind leg	80	76	5(1 + 2): 21
Female leg formulae			
Front leg	49	53	15(1 + 2 + 3)
Middle leg	78	60	4: 22: 37
Hind leg	77	76	6(1 + 2): 18

Pronotum in apterous forms much longer than an eye, rounded on caudal margin, exposing metanotum on sides and behind its rear margin. In macropterous forms the shoulders of pronotum not prominent and caudal angle blunt. *Male:* Anterior trochanter unarmed. Front tibia hairy, as broad distally as base of femur, its longitudinal black ridge on rear distal margin about one fourth length of tibia. Hind trochanter with a number of stout pegs. Hind femur incrassate and armed as shown on Fig. 3, h, i. Hind tibia curved. First genital segment a little longer than last abdominal segment and covered with golden hairs. Last abdominal tergite a little longer than the preceding. Last abdominal ventrite longer than first genital segment and with a low longitudinal carina, transversely concave on ventral surface of first genital segment. Parameres rather large and broad as shown on Fig. 2, j. *Apterous female:* First three connexival segments nearly erect, thereafter erect to slightly overlapping abdominal tergites and first genital which is distinctly depressed. Basal width of last abdominal segment

(dorsally) to its length as 1.5: 2. Hind femur much more slender than in male and armed as shown on Fig. 3, k.

Comparative notes. This black species with yellow to reddish yellow markings is similar in appearance to several other species. However, parameres are long and broad, unlike those of any species that have been figured by Dr. Lundblad. It cannot be *Rh. teretis* Drake, because the species is "neither brownish black" nor "ferrugineous beneath." Moreover, the venter of the male is not brownish black nor "narrowed and sharply ridged ventrally," and the connexiva meet above the seventh segment.

Data on types. Apterous holotype, apterous allotype, morphotype (1 ♂, 2 ♀ ♀ macropterous) plus apterous paratypes (8 ♂ ♂, 3 ♀ ♀) bear following labels: "C. N. H. M. Philippine Zool. Exped. (1946-1947), H. Hoogstraal leg." "Caburan, Caburan, Davao Province, Mindanao, sea level 1:47" and "Small pool beside stream." Also paratypes (7 ♂ ♂, 4 ♀ ♀ apterous), morphotype (3 ♂ ♂, 5 ♀ ♀ macropterous) bear the labels: "C. N. H. M. Philippine Zool. Exped. (1946-47), F. G. Werner leg.," "Barungkot Upi, Cotabato Province, Mindanao, 1500 ft. 47" and "Stream through original forest." Other apterous paratypes (8 ♂ ♂, 8 ♀ ♀) carry the following labels: "C. N. H. M. Philippine Zool. Exped. (1946-1947), H. Hoogstraal," "Mainit, E. slope Mt. Apo, Davao Province, Mindanao, 4300 ft. XI. 46," and "Stream through original forest."

Rhagovelia (Rhagovelia) mindanaoensis n. sp.

(Fig. 5, f to m)

Size	*Length of body*	*Width of head*	*Width of thorax*
Apterous male	2.94 mm.	0.756 mm.	1.18 mm.
Apterous female	2.94 mm.	0.756 mm.	1.26 mm.

Color. Dorsal surface of body black except for a reddish yellow transverse, rectangular spot on anterior margin of pronotum. Antennae and legs black except base of first antennal segment, distal end of acetabula, coxa, trochanter and basal half of front femur, hind coxa and trochanter which are yellow. Thoracic pleura and abdominal venter black, covered with frosty gray.

Structural characteristics.

Male antennal formula: 1st: 2nd: 3rd: 4th:: 38: 20: 28: 21.

Female antennal formula: 1st: 2nd: 3rd: 4th:: 40: 22: 23: 21.

Male leg formulae	*Femur*	*Tibia*	*Tarsus*
Front leg	45	45	15(1 + 2 + 3)
Middle leg	71	57	3: 24: 32
Hind leg	62	63	2.5(1 + 2): 18

Female leg formulae			
Front leg	47	46	15(1 + 2 + 3)
Middle leg	74	56	7: 20: 35
Hind leg	63	70	3(1 + 2): 17

Pronotum much longer than an eye, rounded on caudal margin, exposing metanotum on sides and behind its rear margin. *Apterous male:* Anterior trochanter unarmed. Front tibia moderately hairy, not as broad distally as diameter of femur, with an unusually long black comb-shaped longitudinal ridge on inner margin near distal end. Hind trochanter with or without some small pegs. Hind femur moderately incrassate and armed as shown on Fig. 5, g, and quite hairy. Venter of last abdominal segment bare, with a median longitudinal ridge and a lateral and caudal hairy margin. Venter of first genital segment with a median longitudinal carina as shown on Fig. 5, h. *Apterous female:* Hind femur slightly incrassate with fewer spines than in male. Connexivum flat to obliquely raised. Last abdominal (dorsal) segment short, basal width greater than its length.

Comparative notes. This is a short and broad species like *Rh. minuta* Lundblad, but its parameres (Fig. 5, i, j, k) are entirely different, being not slender and not sigmoid in shape as in *Rh. minuta* (Fig. 1, a).

Data on types. Described from apterous male holotype, apterous allotype and 74 paratypes (32 ♂ ♂, 42 ♀ ♀) bearing the following labels: "C. N. H. M. Philippine Zool. Exped. 1946-47 F. G. Werner leg," "Barungkot, Upi, Cotabato Province, Mindanao 1500 ft. '47" and "Stream through original forest." Also 17 paratypes bearing the labels: "C. N. H. M. Philippine Zool. Exped. (1946-47), H. Hoogstraal leg.," "Caburan Caburan, Davao Province, Mindanao, Sea level 1, '47," and "Small pool beside stream." Holotype, allotype and many paratypes are in the Chicago Natural History Museum. Some paratypes are in Francis Huntington Snow Museum, University of Kansas.

Rhagovelia (Neorhagovelia) hoogstraali n. sp.

(Fig. 4, a to e)

Size	*Length of body*	*Width of head*	*Width of thorax*
Apterous male	3.78 mm.	0.945 mm.	1.51 mm.
Apterous female	3.99 mm.	0.945 mm.	1.51 mm.

Color. Black above. Pronotum with a transverse reddish yellow band behind interocular space of head. The band covers anterior three fourths of pronotum, and this spot is separated from paler

propleura by black band. Venter frosty gray except for prothorax, last abdominal segment and genital segments which may be yellow to brown.

Structural characteristics.

Male antennal formula: 1st: 2nd: 3rd: 4th:: 55: 28: 29: 28.

Female antennal formula: 1st: 2nd: 3rd: 4th:: 48: 23: 26: 25.5.

Male leg formulae	*Femur*	*Tibia*	*Tarsus*
Front leg	58	62	18(1 + 2 + 3)
Middle leg	106	82	6.5: 34: 41
Hind leg	90	98	4(1 + 2): 18
Female leg formulae			
Front leg	52	57	17(1 + 2 + 3)
Middle leg	92	73	3: 32: 39
Hind leg	81	82	2.5 (1 + 2): 20

Pronotum at middle as long as or a little shorter than length of an eye, posterior margin slightly concave. Mesonotum exposing metanotum by a wide margin laterally, and a small margin posteriorly. *Apterous male:* Anterior trochanter unarmed but hairy. Tibia hairy and a little wider at its tip than base, and with a short longitudinal comb of spines on its inner distal end. Hind trochanter armed with one large blunt peg and several small ones. Hind femur incrassate and armed as shown on Fig. 4, b. Pronotum wider than long (57:11). Mesonotum wider than long (55: 42). First genital segment about as long dorsally as last abdominal segment. Parameres symmetrical and shaped as shown on Fig. 4, c. *Apterous female:* Front tibia not as broad distally as in male, and lacks the longitudinal comb-like ridge of male. Trochanter with a single peg. Hind femur slightly thicker than middle femur, and its row of pegs as shown on Fig. 4, d. Connexivum obliquely upturned. Seventh tergite as wide as long, a little longer than sixth tergite at middle.

Comparative notes. The only described species of subgenus *Neorhagovelia* that might some time be taken in the Philippines is *Rh. esakii* Lundblad from "Ishigakijima, Bannadake, Ryukyu Island," but it is not a black species, male hind femur is not greatly incrassate and its armature is different from that in *Rh. hoogstraali.* Parameres are more slender and pointed at distal end.

Data on types. Described from male holotype, female allotype and 19 paratypes (9 ♂ ♂, 10 ♀ ♀) bearing the following labels: "C. N. H. M. Philippine Zool. Exped. (1946-47) H. Hoogstraal," "E. slope Mt. McKinley Davao Province, Mindanao :46," "Stream through original forest." "Elevation 3000 ft." Besides the above

series there is a female bearing the label "C. N. H. M. Philippine Exp. (1946-47) H. Hoogstraal leg," "Mainit, E. slope Mt. Apo, Davao Province, Mindanao 4300 ft. XI," "stream through original forest."

The holotype, allotype and many paratypes are in the Chicago Natural History Museum. Some paratypes are in the Francis Huntington Snow Museum, University of Kansas.

Rhagovelia (Neorhagovelia) werneri n. sp.

(Fig. 4, f to j)

Size	*Length of body*	*Width of head*	*Width of thorax*
Apterous male	3.99 mm.	0.945 mm.	1.51 mm.
Apterous female	4.20 mm.	0.924 mm.	1.57 mm.

Color. Dark brown in dorsal view except anterior two thirds of pronotum and connexivum which are reddish yellow. Antennae and legs dark brown except for basal half of first antennal segment, and bases of front and hind femora which are yellowish to reddish yellow. Venter brown, with a dark brown to nearly black lateral stripe on either side of abdomen which is covered with a pile of silvery hairs.

Structural characteristics.

Male antennal formula: 1st: 2nd: 3rd: 4th:: 51: 25: 34: 32.

Female antennal formula: 1st: 2nd: 3rd: 4th:: 47: 22: 29: 28.

Male leg formulae	*Femur*	*Tibia*	*Tarsus*
Front leg	59	58	17(1 + 2 + 3)
Middle leg	98	80	6: 31: 38
Hind leg	82	80	9(1 + 2): 18
Female leg formulae			
Front leg	51	50	18(1 + 2 + 3)
Middle leg	83	70	4: 31: 31
Hind leg	73	74	10(1 + 2): 18

Pronotum (median length) a little shorter than length of an eye, its rear margin slightly undulate. Mesonotum slightly concave on caudal margin exposing metanotum both caudally and laterally. *Apterous male:* Front trochanter unarmed but hairy. Front tibia hairy, its distal end a little wider than its base. Distal longitudinal comb about three fourths as long as distal tarsal segment. Hind leg armed as shown on Fig. 4, g. Pronotum at middle wider than long (55:16). Mesonotum wider than long (55:30). Genital segments as long as or longer than last abdominal tergite. Parameres symmetrical, and shaped as shown on Fig. 4, h. *Apterous female:* Hind femur not incrassate, its armature as shown on Fig. 4, j. Connexivum with first three segments oblique and remainder

erect. Seventh abdominal tergite with its basal width a little shorter than its length.

Comparative notes. Since this is a brown species with short pronotum we hoped it would prove to be *Rh. esakii* Lundblad. However, it is larger than that species, the male femur is more incrassate and differently armed and the shape of the parameres is different, much shorter and not pointed as in *Rh. esakii.*

Data on types. Described from the apterous male holotype, allotype and 13 paratypes (3 ♂ ♂, 10 ♀ ♀) bearing the following labels: "C. N. H. M. Philippine Zool. Exped. (1946-47) F. G. Werner," "Meran, E. slope, Mt. Apo, Davao Province, Mindanao, P. I. XI 46," and "Original forest 6000 ft. XI 46." Also 83 paratypes (30 ♂ ♂, 53 ♀ ♀ apterous) which bear the following labels: "C. N. H. M. Philippine Zool. Exped. (1946-47), H. Hoogstraal and F. G. Werner leg," "Meran E. slope Mt. Apo, Davao Province, Mindanao 6000 ft. XI 46" and "Stream through original forest." Holotype, allotype and numerous paratypes are in the Chicago Natural History Museum. Some paratypes are in the Francis Huntington Snow Museum, University of Kansas.

Rhagovelia (Neorhagovelia) minutissima n. sp.

(Fig. 5, a to d)

Size	*Length of body*	*Width of head*	*Width of thorax*
Apterous male	2.1 mm.	0.63 mm.	0.798 mm.
Apterous female	2.14 mm.	0.60 mm.	0.84 mm.

Color. In dorsal view, head and rest of body appearing gray, being black covered with gray frost except for a reddish yellow band covering most of anterior two thirds of pronotum behind interocular space of head. Antennae and legs black except basal two fifths of first antennal segment, basal half of front femur, basal fourth of hind femur which are pale yellow. Venter frosty gray except trochanter, coxae, and acetabula which are pale yellow.

Structural characteristics.

Male antennal formula: 1st: 2nd: 3rd: 4th:: 23: 11: 17: 17.

Female antennal formula: 1st: 2nd: 3rd: 4th:: 25: 12: 16: 16.5.

Male leg formulae	*Femur*	*Tibia*	*Tarsus*
Front leg	28	28	9(1 + 2 + 3)
Middle leg	50	37	3: 14: 25
Hind leg	37	34	3(1 + 2): 9
Female leg formulae			
Front leg	30	30	10(1 + 2 + 3)
Middle leg	49	38	5: 15: 24
Hind leg	47	39	3(1 + 2): 9

Pronotum shorter than length of an eye, its rear margin concave and sinuate. Mesonotum large, broadly rounded and medially slightly concave, exposing a uniform band of metanotum on sides and rear. Metanotum and abdominal tergites with more or less complete transverse rows of black spines which are directed backward. Abdominal venter, margin of connexivum and thoracic pleura are also provided with these spines. They are more conspicuous in male than in female. *Apterous male:* Front trochanter unarmed but with some long hairs. Front tibia not broader at apex than at middle. Hind trochanter with two or three small pegs. Hind femur not much incrassate and armed as shown on Fig. 5, b. Connexivum flat. First genital segment about as long as last abdominal tergite. *Apterous female:* First abdominal tergite roundly and transversely elevated; second steeply declivent caudally, third and fourth depressed, fourth laterally, obliquely excavated; fifth laterally excavated to produce a median longitudinal carina, the caudal end of which reaches the higher level of sixth and seventh tergites. Basal three segments of connexivum broad. First one flat, second one starts upward turn that becomes vertical on fourth connexival segment, the edge of which is a crescent-shaped ridge marking the constriction of abdomen at caudal end of fifth abdominal segment, beyond which connexivum is narrow and nearly vertical (see Fig. 5, c).

Comparative notes. Rhagovelia minuta Lundblad was described from a single male specimen from Los Banos, Philippines. The type is 2.8 mm. long. Since Lundblad figured the right paramere which is strikingly different from any other species, we wanted to draw the parameres of this new species. Unhappily the parameres were lost while dissecting for study. However, *Rh. minutissima* is 2.1 mm. long and belongs to a different subgenus. Our description and figures should enable anyone to recognize *Rh. minutissima.*

Data on types. Described from the male apterous holotype, female apterous allotype and one apterous paratype which bear the following labels: "C. N. H. M. Philippine Zool. Exped. (1946-1947) H. Hoogstraal leg.," Dimaniang Busuanga Il. P. I. (Calamianes Group); nr. sea level, III 47," and "Stream through forest."

The holotype and allotype are in the Chicago Natural History Museum. One female paratype is in the Francis Huntington Snow Museum, University of Kansas.

KEY TO THE SPECIES OF RHAGOVELIA FROM THE PHILIPPINES

Apterous males

1. Pronotum long, covering most of mesonotum (subgenus *Rhagovelia*), 2
   Pronotum short, exposing mesonotum (subgenus *Neorhagovelia*) ... 11
2. Size small, less than 3 mm. long ... 3
   Size longer than 3 mm. ... 4
3. Paramere slender, sigmoid in shape with its distal end slightly enlarged (Fig. 1, a) ... *Rh. minuta* Lundblad
   Paramere shorter and broader, its distal end pointed.
   Rh. mindanaoensis Hungerford and Matsuda
4. Color of posterior lobe of pronotum black, somewhat overcast with bluish gray ... 5
   Color of posterior lobe of pronotum brown to very dark brown. If black it is covered with golden hairs ... 7
5. Connexivum entirely black (fide Drake) ... *Rh. philippina* Lundblad
   Connexivum at least margined with yellow or brown ... 6
6. Last abdominal tergite longer than two preceding segments, but shorter than first genital segment. Paramere large and broad.
   Rh. usingeri Hungerford and Matsuda
   Last abdominal tergite shorter than the two preceding segments, but longer than first genital segment. Paramere slender and with a broadened tip ... *Rh. cotabatoensis* Hungerford and Matsuda
7. Size large, at least 4 mm. long ... 8
   Size smaller than 4 mm. long ... 10
8. Venter of abdomen narrowed and sharply ridged ventrally, very densely and rather widely clothed posteriorly with extremely long golden hairs along each side of median longitudinal ridge. First genital segment of male extremely large, very long, with apical two thirds bent strongly downwards ... *Rh. teretis* Drake
   Venter of abdomen not as above ... 9
9. Hind femur with only two large thorns or spines one on ventral side near distal end and the other beyond middle, with small pegs between them, basal area with small numerous pegs (entire rear margin with pegs) (see Fig. 1, b) ... *Rh. luzonica* Lundblad
   Hind femur with six or more large thorns but not at distal end. Underside of femur with long golden hairs.
   Rh. lundbladi Hungerford and Matsuda
10. A yellowish brown spot on anterior lobe of pronotum that does not reach pleura which is gray. Posterior lobe of pronotum black, covered with golden hairs. Slightly thickened hind femur broadest and with a long spine before middle, followed by a row of smaller spines. Parameres broad at base and hairy (Fig. 1, d).
    Rh. orientalis Lundblad
    Anterior lobe of pronotum entirely yellow joining propleura which is also yellow. Posterior lobe brown to dark brown. Hind femur incrassate, armed with two rows of large spines and many small pegs between them. Paramere spatulate and its distal end slightly concave ... *Rh. hoberlandti* Hungerford and Matsuda
11. Very small species, not longer than 2.2 mm.
    Rh. minutissima Hungerford and Matsuda

Much larger species, longer than 3.5 mm. 12

12. A black species. Rear margin of mesonotum medially convex. Paramere as shown on Fig. 4, c. *Rh. hoogstraali* Hungerford and Matsuda
A brown species. Rear margin of mesonotum slightly concave. Paramere as shown on Fig. 4, h. . . . *Rh. werneri* Hungerford and Matsuda

Apterous females

1. Pronotum long, covering most of mesonotum 2
Pronotum short, exposing mesonotum 11
2. Size small, less than 3 mm. long 3
Size large, over 3 mm. long 4
3. Seventh abdominal tergite longer than broad. Connexivum vertical above the end of sixth and all of seventh segment.
Rh. minuta Lundblad
Seventh abdominal tergite broader at base than long. Connexivum only obliquely raised laterally.
Rh. mindanaoensis Hungerford and Matsuda
4. Color of posterior lobe of pronotum black, sometimes overcast with bluish gray 5
Color of posterior lobe of pronotum brown to very dark brown. If black it is covered with golden hairs 7
5. Connexivum entirely dark ..... *Rh. philippina* Lundblad
Connexivum at least margined with yellow or brown 6
6. Last abdominal tergite rather broad, its basal width to its length as 3:4 ..... *Rh. usingeri* Hungerford and Matsuda
Last abdominal tergite rather narrow, its basal width to its length as 1:3 ..... *Rh. cotabatoensis* Hungerford and Matsuda
7. Size large, at least 4 mm. long 8
Size smaller 10
8. Connexivum strongly reflexed inward posteriorly, meeting above seventh segment, then continuing in contact to near apex, apex acuminate or projecting posteriorly ..... *Rh. teretis* Drake
Connexivum not reflexed to meet above seventh segment 9
9. "Hind femur of female slender, with a few short spines within apically" (Drake). Connexivum yellowish, margined with brownish black ..... *Rh. luzonicus* Lundblad *
9. Hind femur with two long spines, the longer one before middle and the other half way between it and distal end of femur, with ten or more short pegs between the longer spine and the distal end of femur and one short spine between the long spine and base of femur. Connexivum basally brown, with a median longitudinal band of yellow and brown margin ..... *Rh. lundbladi* Hungerford and Matsuda
10. A yellowish brown spot on anterior lobe of pronotum that does not reach pleura which is gray. Posterior lobe black, covered with golden

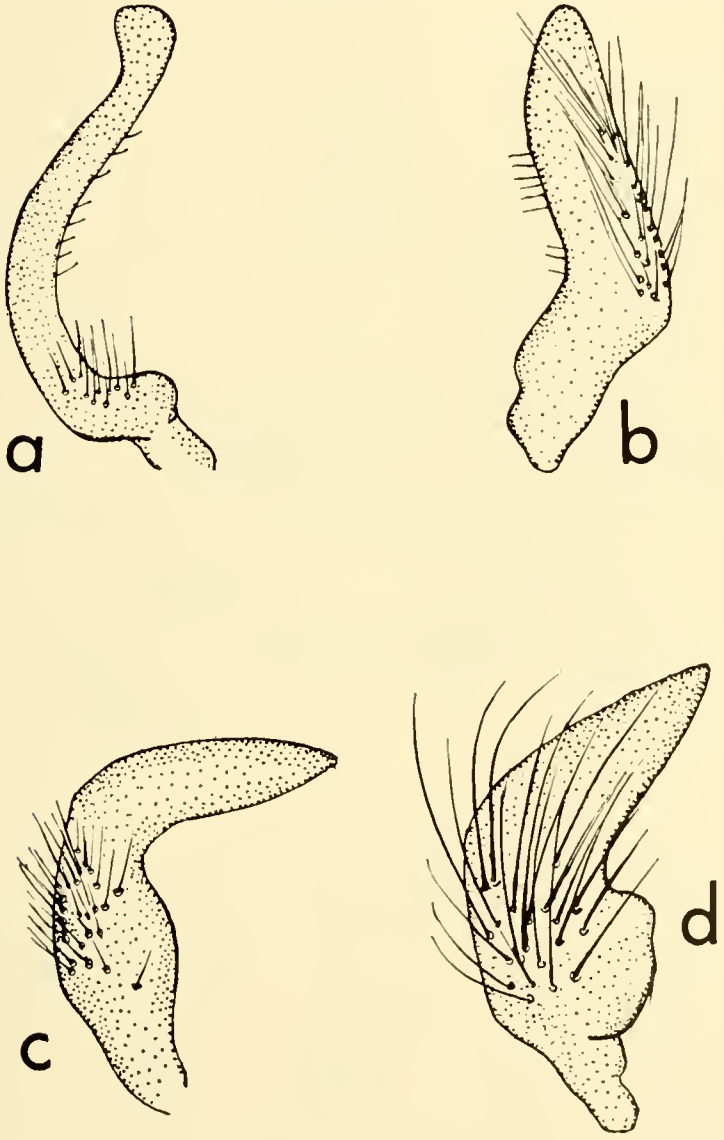
* *Rh. luzonica* Lundblad was described from a single macropterous male from Los Baños, N. Luzon. In 1948 Dr. Drake received one apterous male and six apterous females taken from a river near Baguio, Luzon, and gave a brief description of them. Since he had a male his determination should be correct, but he did not mention the length of his specimens which should be shorter than the macropterous type. The seventh abdominal tergite was not described for the female.

hairs ..... *Rh. orientalis* Lundblad
Anterior lobe of pronotum entirely yellow, joining propleura which is also yellow ..... *Rh. hoberlandti* Hungerford and Matsuda

11. Very small species, not longer than 2.2 mm.
Rh. minutissima Hungerford and Matsuda
Much larger species, longer than 3.5 mm. 12

12. A black species. Rear margin of mesonotum medially convex.
Rh. hoogstraali Hungerford and Matsuda
A brown species. Rear margin of mesonotum medially concave.
Rh. werneri Hungerford and Matsuda

FIGURE 1



a. Right paramere of *Rh. minuta* Lundblad (1936)
b. Left paramere of *Rh. luzonica* Lundblad (1937)
c. Right paramere of *Rh. philippina* Lundblad (1936)
d. Right paramere of *Rh. orientalis* Lundblad (1937)

(copied from Lundblad)

FIGURE 2

FIG. 2. *Rhagovelia lundbladi* n. sp. a to f.

a. Dorsal view of apterous male.
b. Hind leg of male.
c. Underside of base of hind femur of male.
d. Left paramere.
e. Hind leg of female.
f. Last dorsal abdominal segments of female.

Rhagovelia hoberlandti n. sp. g to l.

g. Dorsal view of apterous male.
h. Hind leg of male, showing the large spines on tibia.
i. Underside of left hind femur of male.
j. Left paramere.
k. Last dorsal abdominal segments of female.
l. Hind leg of female.

FIGURE 2

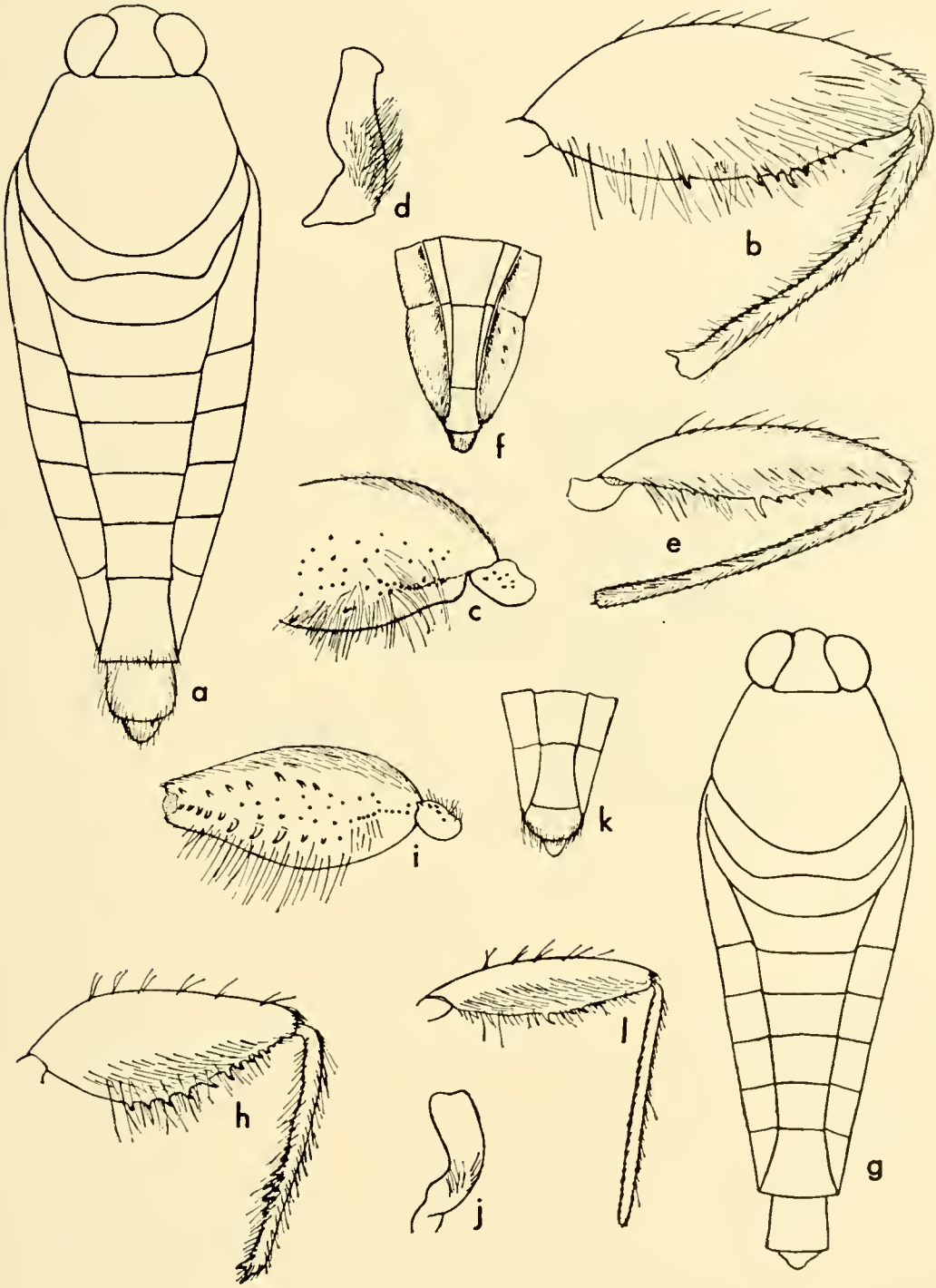


FIGURE 3

FIG. 3. *Rhagovelia cotabatoensis* n. sp. a to f.

a. Dorsal view of apterous male.
b. Hind leg of male.
c. Underside of base of hind femur of male.
d. Left paramere.
e. Hind leg of female.
f. Last dorsal abdominal segment of female.

Rhagovelia usingeri n. sp. g to l.

g. Dorsal view of apterous male.
h. Hind leg of male.
i. Underside of base of hind femur of male.
j. Left paramere.
k. Hind leg of female.
l. Last dorsal abdominal segments of female.

FIGURE 3

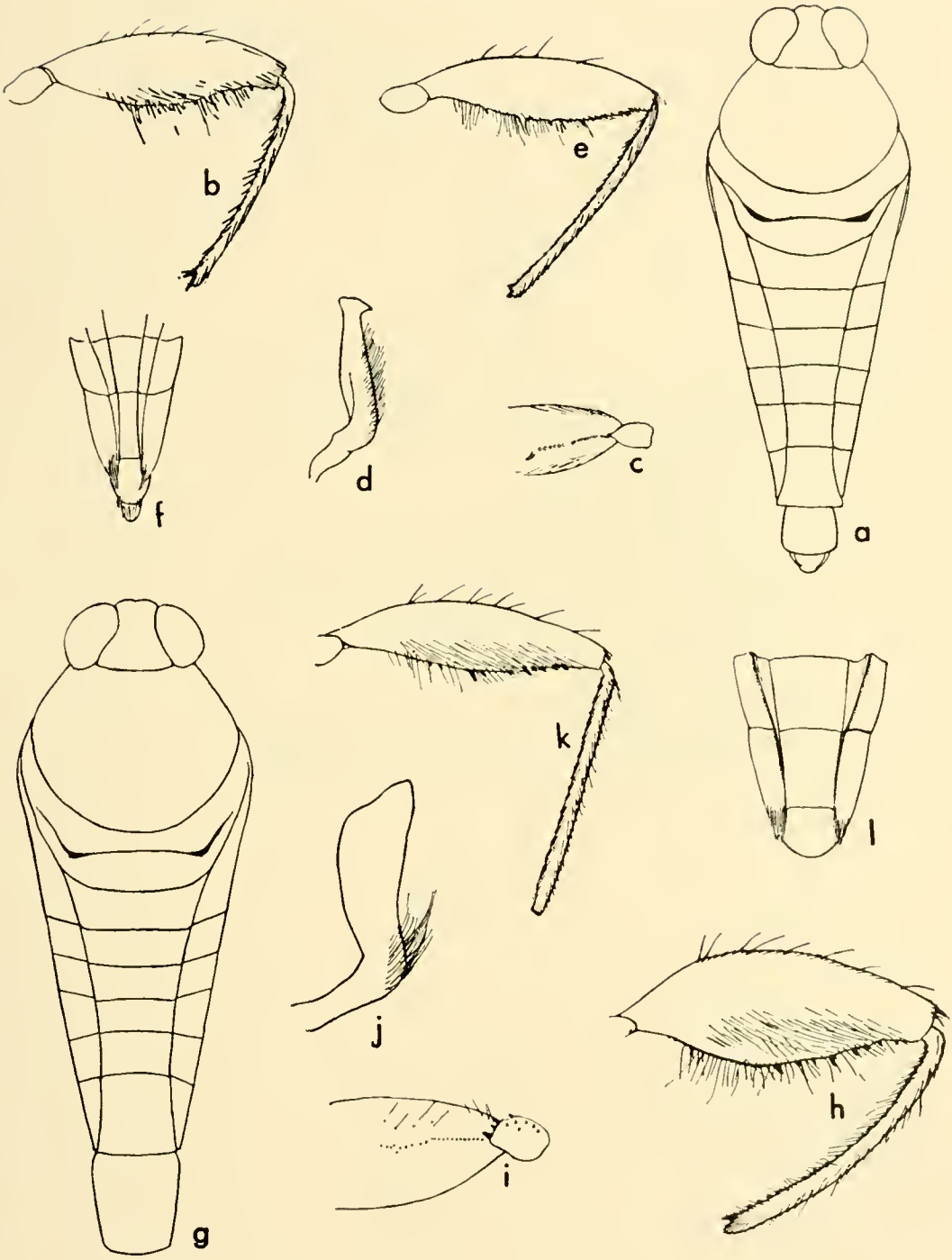


FIGURE 4

FIG. 4. *Rhagovelia (Neorhagovelia) hoogstraali* n. sp. a to e.

a. Dorsal view of apterous male.
b. Hind leg of male.
c. Left paramere.
d. Hind leg of female.
e. Last dorsal abdominal segments of female.

Rhagovelia (Neorhagovelia) werneri n. sp. f to j.

f. Dorsal view of apterous male.
g. Hind leg of male.
h. Left paramere.
i. Hind leg of female.
j. Last dorsal abdominal segments of female.

FIGURE 4

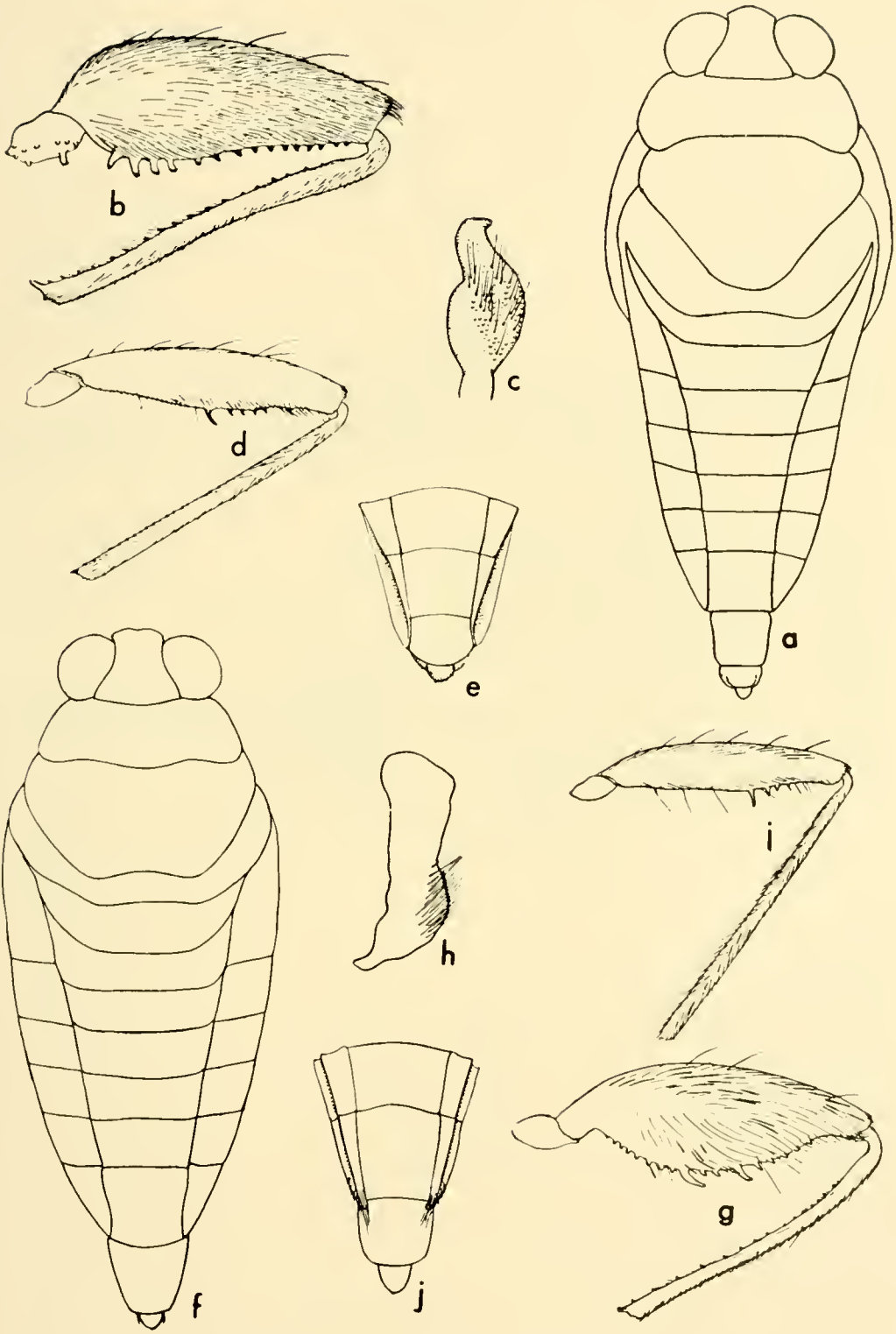


FIGURE 5

FIG. 5. *Rhagovelia (Neorhagovelia) minutissima* n. sp. a to d.

a. Dorsal view of apterous male. Note the short spines on the lateral margin of the connexivum and across the abdominal tergites.
b. Hind leg of male.
c. Dorsal view of apterous female.
d. Hind leg of female.

Rhagovelia (Rhagovelia) mindanaoensis n. sp. f to m.

f. Dorsal view of apterous male.
g. Hind leg of male.
h. Venter of last abdominal and genital segments of male.
i, j, k. Various views of the right paramere.
l. Hind leg of female.
m. Last dorsal abdominal segments of female.

FIGURE 5

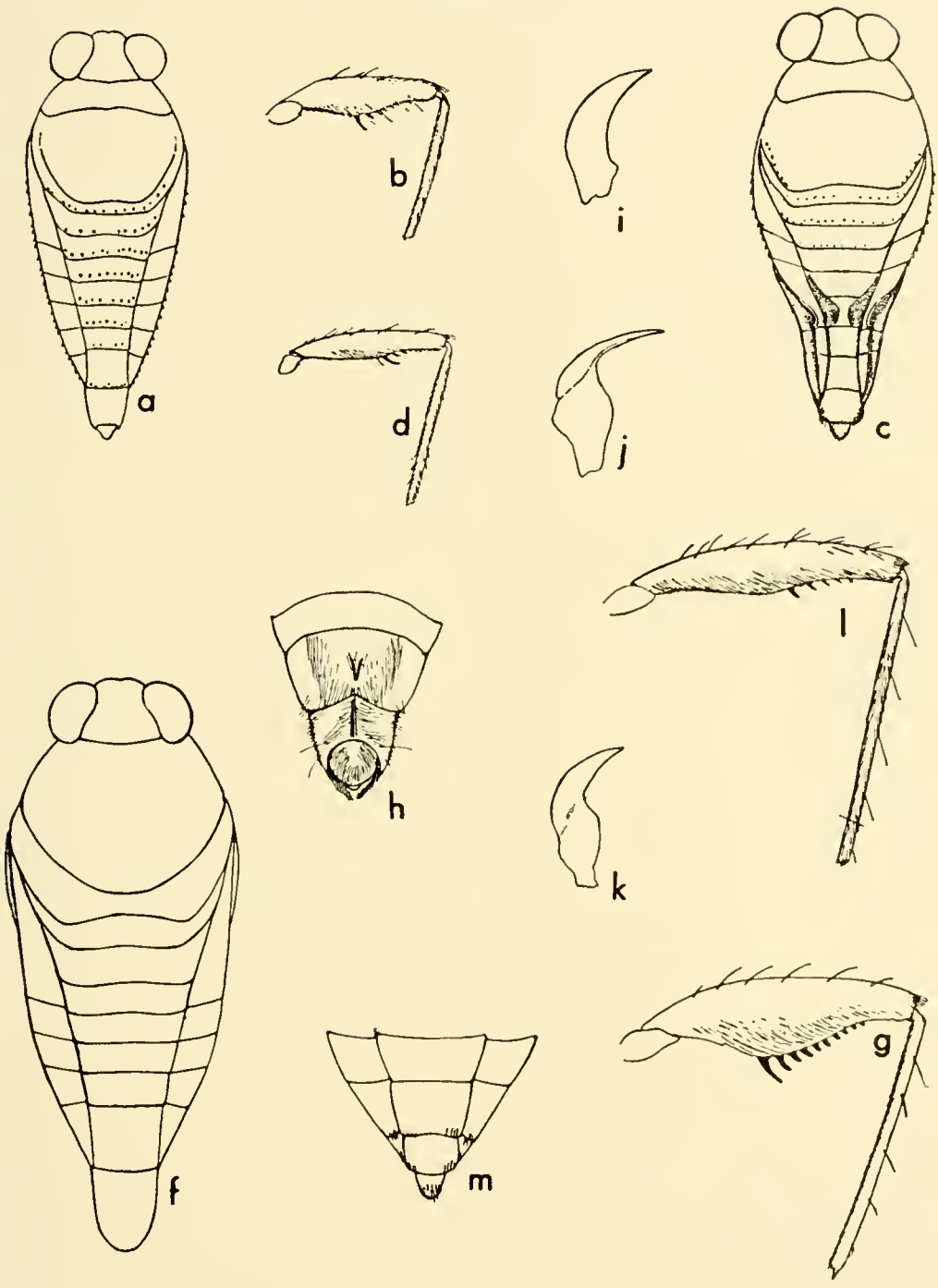


Fig. 1. *Melissodes (Eumelissodes) coreopsis* Robertson collecting pollen and nectar from *Helianthus* sp. in Kansas (photograph by Dr. Delma E. Harding, Iowa State University of Science and Technology, Ames, Iowa).

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A Revision of the Bees of the Genus *Melissodes* in North and Central America. Part III (Hymenoptera, Apidae) *

BY

WALLACE E. LABERGE

ABSTRACT: This is the third and last part of a monographic revision of the bee genus *Melissodes* in North and Central America. Eighty-five species belonging to two subgenera are described. One subgenus, *Callimelissodes*, is newly described. Thirty-nine new species are described:

Melissodes limbus, M. lustra, M. pilleata, M. elegans, M. tincta, M. subillata, M. gelida, M. terminata, M. bicolorata, M. bimatris, M. minuscula, M. hurdi, M. brevipyga, M. relucens, M. exilis, M. vernalis, M. utahensis, M. monoensis, M. nigracauda, M. comata, M. fasciatella, M. cerussata, M. fumosa, M. perpolita, M. paulula, M. expolita, M. pexa, M. micheneri, M. appressa, M. interrupta, M. lutulenta, M. ochraca, M. paucipuncta, M. plumosa, M. clarkiae, M. rufipes, M. pullatella, M. crocina, M. tribas. Fifty-four names are relegated to synonymy and six names remain as *nomina dubia.* In an addendum, an additional new species, *M. haitiensis*, belonging to subgenus *Ecplectica* (treated in the first part of this revision, LaBerge, 1956) is described.

INTRODUCTION

This is the third part of a revision of the bees of the genus *Melissodes* in North and Central America. The key to the subgenera of the genus *Melissodes* published in the first part of this revision (LaBerge, 1956) is repeated herein in modified form. A total of 30,095 specimens representing 86 species have been examined for this part of the revision.

Explanations of the methods used in describing the species, the meanings of certain descriptive terminology and methods used in taking certain measurements are described in a section on descriptive methodology in the first part of this revision (LaBerge, 1956,

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This study was begun in the Department of Entomology, The University of Kansas, Lawrence, Kansas.

p. 919). No important changes in methodology have been introduced into this part of the revision.

The reader is also referred to the first part of this revision for a complete list of acknowledgements. I wish to thank the Society of the Sigma Xi for a Grant-in-Aid of Research which enabled me to travel in Europe during the summer of 1957 in order to study the type specimens now located in European museums. Certain persons have rendered special aid in comparing specimens, in graciously lending types in their care and in generously giving of their time and advice. I wish to especially thank the following persons for these services: Dr. I. H. H. Yarrow of the British Museum (Natural History), London; Mr. Karl V. Krombein of the United States National Museum, Washington, D. C.; Mr. P. H. Timberlake, Citrus Experiment Station, Riverside, California; and Dr. T. B. Mitchell, North Carolina State College, Raleigh, North Carolina. I am grateful to Dr. C. D. Michener of the University of Kansas, Lawrence, Kansas, for his interest and guidance throughout the period of preparation of this revision and for reading and commenting upon the manuscript.

The Research Council of the University of Nebraska, Lincoln, Nebraska, is especially thanked for a grant (1960) which helped to defray the expenses of preparing the drawings and maps and the typing of the manuscript. Thanks are due also to the Kansas University Endowment Association for a grant (1953) which permitted the author to visit various museums in the United States for the purpose of studying type specimens and for another grant (1955) which helped defray costs of preparing illustrative material.

PHYLOGENETIC RELATIONSHIPS OF THE SUBGENERA

A diagram showing the relationships of the various subgenera of the genus *Melissodes* was published in the first part of this revision (LaBerge, 1956, p. 915). That diagram included three subgenera not now included in the genus *Melissodes* (*Brachymelissodes*, *Epimelissodes*, and *Idiomelissodes*, now in genus *Svastra* Holmberg). Also, the diagram did not include a subgenus subsequently recognized and described below (*Callimelissodes*). New characters have since been discovered which shed new light on the relationships of the subgenera now included in the genus. Therefore, a new analysis of these relationships is presented here.

From among the many characters found to be useful in the taxonomy of the genus *Melissodes* nineteen were chosen on the bases that they show variation among the subgenera and that the

primitive versus the specialized condition of each could be logically inferred. These characters and their primitive and specialized states are listed below.

Primitive Characters	*Specialized Alternatives*
1. Female sixth tergum with lamelliform, toothed lateral parts of gradulus.	1. Lateral parts of gradulus absent or cariniform.
2. Male with five-segmented maxillary palpi at least occasionally.	2. Four- or three-segmented maxillary palpi.
3. Male seventh sternum with lateral plates small, flat, hairy below.	3. Male seventh sternum otherwise.
4. Propodeum of female longer than metanotum medially.	4. Propodeum of female shorter or no longer than metanotum medially.
5. Clypeus flat; mouthparts relatively short.	5. Clypeus more or less bowed out; mouthparts relatively long.
6. Male antennae long, first segment at most one-third as long as second segment.	6. Male antennae short; first segment more than one-third of second.
7. Scopal hairs branched.	7. Scopal hairs simple or weakly branched.
8. Galeae with hairs straight.	8. Galeae with hooked hairs.
9. Galeae shiny or at most lightly shagreened.	9. Galeae dulled by dense tessellation.
10. Integument of mesoscutum shiny to shagreened.	10. Mesoscutum densely tessellate.
11. Distal pale bands of terga 2 and 3 not apical or at least not completely so.	11. Distal pale bands of terga 2 and 3 apical.
12. Male fifth sternum with apical margin straight to concave.	12. Male fifth sternum convex medially to produced.
13. Male clypeus yellow or largely yellow or cream-colored.	13. Male clypeus black or largely black.
14. Size of bee medium.	14. Size small or large.
15. Female with distal pale band of tergum 2 present, interrupted or not, if interrupted or absent, band of tergum 4 also interrupted or absent.	15. Female with distal pale band of tergum 2 absent or broadly interrupted while that of tergum 4 uninterrupted.
16. Eyes converge towards mandibles.	16. Eyes subparallel to converging towards vertex.
17. Male flagellar segments without shiny elongate depressions.	17. Flagellar segments with shiny elongate depressions.
18. Gonostylus with short, simple or barbed, diffuse hairs.	18. Gonostylus with hairs long, simple, more or less concentrated near base on outer surface.
19. Male sternum 8 with simple or bidentate ventral tubercle.	19. Male sternum 8 with strong medioventral crest.

All eight subgenera are specialized for all included species in at least two of these and primitive in at least ten of these characters. Each subgenus (except the monotypic *Psilomelissodes*) may have one or more species which is specialized in one or more characters, whereas the other species of the same subgenus are primitive for the same characters. Thus, for each character a subgenus may be primitive, partly specialized, or specialized. The subgenera and the number of the characters listed above are summarized in table I. In this table a specialized condition is represented by a plus sign, a primitive condition by a zero, and a partly specialized character by a dash. The number of each condition is tabulated for each subgenus at the bottom.

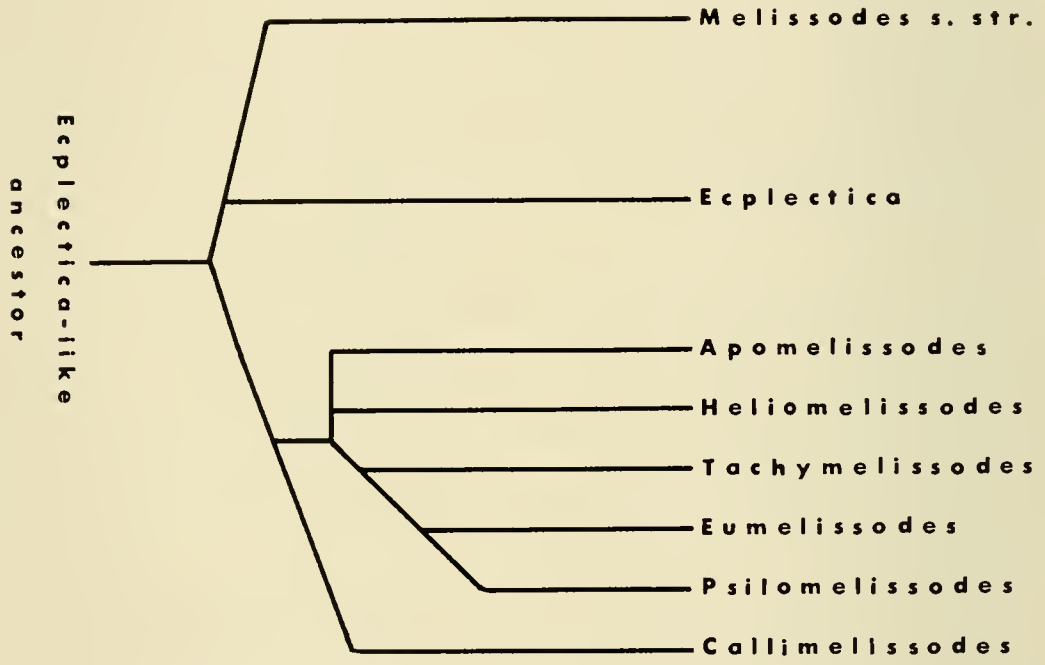

FIG. 2. Dendogram showing the relationships of the subgenera of *Melissodes* Latreille. The lengths of the various lines are of no significance.

The phylogenetic diagram (Fig. 2) is based upon the above facts plus special consideration of the characters. An example of the latter is the dichotomy shown in the diagram between *Ecplectica-Melissodes* and the other subgenera. Although *Melissodes s. str.* appears specialized in more characters and at least as primitive as is the subgenus *Eumelissodes*, it is shown as having been derived from an *Ecplectica*-like ancestor independently of the *Eumelissodes* and the other subgenera. This dichotomy can also be seen in the list of characters given above. *Melissodes s. str.* has certain specialization of the male terminalia (characters 18 and 19) which can be more logically derived from the condition in *Ecplectica* than

TABLE I. Nineteen Characters of the Subgenera of *Melissodes*.

CHARACTERS BY NUMBER	Subgenera							
	Eoplectica	Melissodes s. str.	Eumelissodes	Callimelissodes	Apomelissodes	Heliomelissodes	Psilomelissodes	Tachymelissodes
1.	0	0	+	+	+	+	+	+
2.	+	—	—	+	+	+	+	+
3.	0	+	+	+	+	+	0	+
4.	+	+	0	0	0	0	0	0
5.	0	0	0	0	+	+	0	0
6.	0	0	0	0	0	0	+	+
7.	0	0	0	—	—	0	+	0
8.	0	0	—	—	—	0	0	0
9.	0	0	—	—	0	0	0	0
10.	0	—	0	0	0	0	0	0
11.	0	0	0	0	+	0	+	+
12.	0	0	0	+	0	0	0	0
13.	0	0	—	0	—	—	+	—
14.	—	—	—	—	0	0	0	+
15.	+	0	0	0	0	0	0	0
16.	0	0	0	0	—	+	0	0
17.	0	0	—	—	0	0	0	0
18.	0	+	0	0	0	0	0	0
19.	0	+	0	0	0	0	0	0
Totals..... 0	15	12	11	10	10	13	13	12
—	1	3	6	5	4	1	0	1
+	3	4	2	4	5	5	6	6

from that in *Eumelissodes*. The condition of the same two characters in *Eumelissodes* can also be more logically derived from *Ecplectica* than from *Melissodes s. str.* Also, *Ecplectica* and *Melissodes s. str.* share a specialization (character 4) which separates them from the remaining subgenera and, vice versa, the remaining subgenera share a specialization (character 1) not yet acquired by the former two subgenera.

In spite of these considerations, the true phylogenetic picture could still be with a *Eumelissodes*-like ancestor giving rise to *Eumelissodes* and its related subgenera on one hand and to *Melissodes s. str.* through *Ecplectica* on the other hand. This hypothesis lacks the merit of having the evidence of primitiveness of the chosen phylogenetic arrangement. That is, the subgenus *Ecplectica* shows the primitive alternative in 15 of the 19 characters, whereas *Eumelissodes* is primitive in 11 of the 19 characters.

KEY TO THE SUBGENERA OF NORTH AND CENTRAL AMERICAN MELISSODES

The following key is an adaptation of that given by LaBerge (1956, p. 920). This key was modified by LaBerge (1956, p. 545) to include an additional species in the subgenus *Apomelissodes*. It is here further modified to omit those subgenera which have been removed from the genus *Melissodes* (*e. g., Epimelissodes, Brachymelissodes,* and *Idiomelissodes*) and to include the new subgenus described below (*Callimelissodes*).

The subgenera of *Melissodes* are extremely difficult to key, especially in the female sex. Therefore, some subgenera appear several times in the following key in order to include aberrant species. The males key out readily if one uses genitallic characters, otherwise certain subgenera must appear more than once in the key. The subgenera *Ecplectica* and *Melissodes* key out together in the female sex, partly because it is difficult to separate these subgenera in that sex and because in the original treatment of the species of these subgenera (LaBerge, 1956) the species are placed in the same key.

MALES

1. Clypeus protruding beyond eye from ½ to ¾ width of eye in profile; metasomal terga 2-5 fringed with narrow marginal bands of appressed white pubescence, bands much narrower than basal areas; antennae long, minimum length first flagellar segment equals less than ⅓ maximum length second segment ..... *Apomelissodes*

Clypeus usually not protruding beyond eye by as much as half width of eye in profile, *if* protruding by half width of eye or more, *then* minimum length first flagellar segments equals ⅓ or more of maximum length second segment; terga often not fringed by pubescent bands, but bands when present interrupted medially and/or subapical 2

2 (1). Posterior margin of fourth and usually third sternum broadly convex, or produced into a broad, thin, hyaline, colorless flap ..... *Callimelissodes*

Posterior margins of third and fourth sterna straight to slightly concave, never produced into a flap 3

3 (2). Clypeus strongly protruding beyond eye by ¾ or more of width of eye in profile; maximum length first flagellar segment equals 0.4 or more of maximum length second segment ..... *Heliomelissodes*

Clypeus usually protruding half or less of width of eye in profile, *if* protruding more, *then* maximum length first flagellar segment less than 0.4 of maximum length second segment 4

4 (3). Maximum length first flagellar segment as long as or almost as long as maximum length second segment and longer than third segment (antennae femalelike); clypeus wholly black ..... *Psilomelissodes*

Maximum length first flagellar segment shorter than maximum length second segment and distinctly shorter than third; clypeus usually pale, occasionally partly or wholly black 5

5 (4). Minimum length first flagellar segment distinctly more than half maximum length second segment; terga 2-5 with pubescent bands apical, subequal in width across each tergum and subequal in width to each other ..... *Tachymelissodes*

Minimum length first flagellar segment half of maximum length second segment or less; terga 2-4 with pale pubescent bands usually not all apical or subequal in width, often interrupted medially and usually subapical 6

6 (5). Characters of genitalia and hidden sterna 7

External characters 9

7 (6). Median apical plates sternum 7 without hairs on ventral surfaces, usually small, curled ventrally along an oblique axis to form half or more of an oblique cylinder or scroll, but often secondarily flattened and expanded, or secondarily reduced in size ..... *Melissodes*

Median plates sternum 7 thin, hyaline, with short to moderately long hairs on ventral surfaces, not curled ventrally, relatively large 8

8 (7). Gonostylus short, less than half as long as gonocoxite, in lateral view twice as broad or more near base as near apex, narrowing abruptly near middle, not capitate; median

plates sternum 7 relatively small, with several short hairs ventrally ..... *Ecplectica*

Gonostylus short to long, usually as long as or longer than half length of gonocoxite, in lateral view not twice as broad near base as near apex, often somewhat capitate; median plates sternum 7 large, with abundant short to moderately long hairs ventrally ..... *Eumelissodes*

9 (6). Terga 2-5 without pale pubescent bands or these all interrupted medially, *if* one or two bands are complete, *then* thoracic hairs mostly black, or black and white mixed, and labrum all or almost all pale-colored ..... *Melissodes*

Terga 2-5 usually with complete bands, occasionally one or more absent or interrupted medially, *if* with only one or two bands complete, *then* thorax bright ferrugineous hairs and labrum all or mostly all black 10

10 (9). Labrum wholly pale; mandibles usually with basal yellow spots; last two metasomal terga with dark brown to black hairs 14

Labrum with at least a dark margin and mandibles often without pale basal spots, *or* last two metasomal terga with only pale hairs, *or* both 11

11(10). Galeae smooth and shiny, without tessellation or shagreening except at tips 12

Galeae dulled by tessellation or shagreening at least in apical half ..... *Eumelissodes*

12(11). Last two terga with dark brown to black hairs 13

Last two terga with pale hairs only ..... *Eumelissodes*

13(12). Margins of terga 2-4 broadly hyaline, colorless or nearly so, *or* labrum entirely dark *or* pale spot covers less than half of surface, or both ..... *Eumelissodes*

Margins of terga 2-4 opaque, black to reddish-brown; labrum mostly pale-colored, at most with narrow apical margin brown to black ..... *Melissodes*

14(10). Tergum 2 with distal pale band complete or only narrowly interrupted medially, *if* broadly interrupted, *then* basal pale band indistinct, consisting of diffuse pubescence or partly or wholly dark pubescence ..... *Melissodes*

Tergum 2 with distal pale band absent or broadly interrupted medially, each fascia equal to ⅓ or less width of tergum, with basal pale band distinct ..... *Ecplectica*

FEMALES

1. Scopal hairs simple or weakly branched, *if* weakly branched, *then* clypeus in profile protruding beyond eye by ⅔ width of eye or more; pygidial plate not narrow ..... *Apomelissodes*

Scopal hairs branched, usually abundantly so, *if* weakly branched, *then* clypeus in profile not protruding beyond eye by as much as ⅔ width of eye 2

2 (1). Clypeus protruding anteriorly beyond eye in profile by ½ to ⅔ width of eye; inner orbits of eyes often parallel; inner sur-

faces hind basitarsi with hairs dark brown to black (scopal hairs highly plumose, often yellowish) ..... *Heliomelissodes*

Clypeus protruding beyond eye by less than half width of eye in profile, *if* protruding as much as half width of eye, *then* inner orbits of eyes distinctly converging towards mandibles and/or inner surfaces of hind basitarsi with hairs bright red to yellow (scopal hairs occasionally weakly branched) 3

3 (2). Scopal hairs weak, with few branches, not hiding outer surfaces of hind basitarsi and tibiae; metasomal terga very sparsely and weakly punctate, dulled by dense, fine shagreening and weakly banded with sparse pubescence and hairs; pygidial plate V-shaped with broadly rounded apex ..... *Psilomelissodes*

Scopal hairs strongly branched and hiding outer surfaces of basitarsi and tibiae; or, *if* weak and with few branches, *then* terga coarsely punctate at least basally, or moderately shiny to shiny and strongly banded with abundant pubescence and hairs, *or* pygidial plate narrowly U-shaped 4

4 (3). Scopal hairs with only one or two braches on each side of rachis; pygidial plate narrow, U-shaped ... *Callimelissodes*

Scopal hairs more highly plumose, most hairs with three or more branches on each side of rachis; pygidial plate variable, usually V-shaped with acute or well-rounded apex, 5

5 (4). Terga 2-4 with distal pale pubescent bands reaching apical margins of terga, of about same width across each tergum and subequal in width to each other, not arising from distinct punctures, as narrow or narrower than basal area of dark pubescence ..... *Tachymelissodes*

Terga 2-4 with distal pale pubescent bands, or at least tergum 2, not reaching apices of terga, or, *if* reaching apices of terga, *then* diffuse over entire tergum or much wider than basal area of dark pubescence and/or not of about the same width across each tergum or subequal in width to each other; tergal punctures variable 6

6 (5). Last flagellar segment as long as broad or slightly shorter, about equal to penultimate segment in length, *or*, small bees, 8-9 mm. in length with galeae with abundant long hooked hairs above or with sparse, extremely short, blunt, straight hairs and regular dense tessellation .... *Callimelissodes*

Last flagellar segment longer than broad and longer than penultimate segment; small to large bees, *if* small, *then* galeae either with abundant long straight hairs, or surface not densely tessellate, never small and with abundant hooked hairs 7

7 (6). Sides of thorax and propodeum with black hairs; first tergum with sparse punctures above, medially restricted to basal third of tergum except a few widely scattered punctures; galeae shiny; terga 2 and 3 with interband zones with sur-

faces dulled by fine, dense, reticulotransverse shagreening ..... *Callimelissodes*

Sides of thorax and propodeum with pale hairs, or, *if* with dark hairs, *then* first tergum densely punctate above at least in basal half, and/or galeae dulled by shagreening or tessellation; occasionally terga 2 and 3 with interband zones with surfaces shiny, unshagreened 8

8 (7). First metasomal tergum with extremely sparse punctures restricted to basal third of tergum or less medially; *either* small to medium-sized bees with pygidial plate narrow, subparallel-sided and about twice as long as median width, *or* large bees with hairs of inner surface hind basitarsi black and of lower-lateral surfaces of thorax black, *Callimelissodes*

First metasomal tergum with punctures usually abundant at least in basal half, *if* sparse and restricted to basal third or less, *then* medium-sized bees with pygidial plate broadly V-shaped and much shorter than twice median width and lower-lateral surfaces of thorax without dark hairs 9

9 (8). Large bees, wings deep brown, inner surfaces hind basitarsi with hairs dark brown, mesoscutum with large patch of dark brown hairs; head and thorax coarsely punctate, genal area near lateral margin of eyes with punctures round, deep, separated by about one puncture width or less, *Callimelissodes*

Size variable, *if* large, *then* wings not deep brown, *or* hairs of inner surface hind basitarsi yellow to red, *or* mesoscutum with at most small patch of brown hairs; head and thorax less coarsely punctate, genal area near lateral margin of eye with punctures usually minute, separated by much more than one puncture width 10

10 (9). Metasomal tergum 6 with postgradular carina with lateral parts lamelliform and ending abruptly in a short blunt tooth; pygidial plate narrow in apical half, often with sides subparallel (unless worn); tibial plate short, with edges exposed except anteriorly and on lower, anterior angle ..... *Callimelissodes*

Metasomal tergum 6 with postgradular carina with lateral parts absent or at most cariniform, never with tooth; pygidial plate short, broad, not narrowed in apical half, not subparallel-sided; tibial plate larger, hairs cover edge anteriorly and at least on anterior half of lower margin (unless worn) 11

11 (10). Lateral and ventral surfaces of thorax with dark brown hairs (including propodeum); terga 2 and 3 with lateral raised areas of interband zones with large, irregular piliferous punctures, surfaces very shiny, with no tessellation or shagreening; supraclypeal area with surface smooth and shiny, unshagreened ..... *Eumelissodes*

Lateral surfaces of thorax with pale hairs at least in some restricted area, *or* terga 2 and 3 with raised areas with surfaces at least delicately shagreened; supraclypeal area often dulled by shagreening or tessellation 12

12(11). Eye narrower than genal area in profile, widest part of eye equals half or less of length; lateral and ventral surfaces of thorax with black hairs ..... *Eumelissodes*

Eye wider than or equal to genal area in profile, widest part of eye usually equals more than half length, *or*, lateral surfaces of thorax with all or almost all hairs pale 13

13(12). Hairs of thorax all or almost all black; galeae shiny, without shagreening or tesselation, except at tips, *Melissodes* and *Ecplectica*

Hairs of thorax largely pale, *or* galeae moderately shiny to dull due to shagreening or tesselation or both 14

14(13). Second flagellar segment longer than wide ventrally; inner surfaces hind basitarsi with hairs brown to black, *Eumelissodes*

Second flagellar segment as long as wide or shorter, *or* inner surfaces hind basitarsi with hairs red to yellow, or both .. 15

15(14). Vestiture of metasomal terga entirely black or dark brown, except long hairs of first tergum and occasionally a thin median pale pubescent band on tergum 2; dorsum of thorax with rufescent to ochraceous hairs .... *Eumelissodes*

Terga with various amounts and arrangements of pale pubescence, never entirely dark except first and second terga, *or* dorsum of thorax with abundant dark hairs, or both .. 16

16(15). Metasomal tergum 3 *either* (a) with marginal area covered by pale pubescent band or nearly so (except median triangular notch less than ⅓ width of tergum), *or* (b) with an impunctate apubescent margin which either markedly narrows laterally from a median notch or is narrower than the pale pubescent band of tergum 2 across the entire tergum ..... *Eumelissodes*

Metasomal tergum 3 with (a) dark hairs apical to distal pale band across median third or more of tergum, *or* (b) with pale hairs in apical area not completely hiding surface and having fewer and shorter branches and more erect than those of distal pale band (note punctures when these are worn), *or* (c) with apical apubescent area wider than distal pale band of tergum 2 across entire tergum .. 17

17(16). Galeae above moderately shiny to dull, with shagreening or tessellation in at least apical half 18

Galeae above smooth and shiny, without shagreening or tessellation except at tips 19

18(17). Metanotum medially as long as dorsal face of propodeum or longer; tergum 2 with distal pale band almost never interrupted medially, with straight anterior margin and evenly curved posterior margin; tergum 1 usually only narrowly hyaline or not at all, *if* broadly hyaline, *then*

clypeus without large shiny median boss and inner surfaces hind basitarsi with hairs red to yellow ..... *Melissodes*

Metanotum medially distinctly shorter than dorsal face of propodeum, *or, either* distal pale band of tergum 2 interrupted medially or notched along posterior margin, *or* first tergum broadly hyaline, clypeus with large shiny median boss and inner surfaces hind basitarsi with hairs dark brown to black ..... *Eumelissodes*

19(17). Dorsal face of propodeum usually without distinct punctures, irregularly rugose, occasionally with small scattered punctures apically but these obscured by dense tessellation and basal half to three-fourths irregularly rugose, *Eumelissodes*

Dorsal face of propodeum with distinct punctures in at least apical half, ground areas tessellate but not so densely as to obscure punctures, basal half (or less) punctate or reticulorugose, not irregularly so 20

20(19). Tergum 2 with distal pale pubescent band uninterrupted medially, evenly curved along posterior margin and of about the same width across tergum ..... *Melissodes*

Tergum 2 with distal pale pubescent band absent or interrupted medially, *or* not evenly curved along posterior margin but conspicuous notched medially 21

21(20). Tergum 2 with distal pale band absent or broadly interrupted medially, the lateral fasciae thus formed well separated from apical margin of tergum and each fascia no broader medially than half width of apical area, *Melissodes* and *Ecplectica*

Tergum 2 with distal pale band at most narrowly interrupted and lateral fasciae thus formed each much broader than half width of apical area medially ..... *Eumelissodes*

Callimelissodes, new subgenus

Type species. Melissodes lupina Cresson, 1878.

This is a moderate-sized North American subgenus previously confounded with the subgenus *Eumelissodes* LaBerge by the author because of the lack of dependable female characteristics. *Callimelissodes* is predominantly a western North American subgenus containing fourteen species, only one of which extends in range east of the prairie states. The following description is in the style of that given by LaBerge (1956, p. 1177) for *Eumelissodes.*

Female. Small to large bees; integument generally black. *Clypeus flat to slightly protuberant, never protruding beyond eyes by as much as half width of eye in profile;* eyes converging toward mandibles, usually about three-eighths as broad as long, and in profile as broad as or broader than genal area; minimum length of first flagellar segment variable, in one species ultimate segment no longer than broad; *galeae shiny and unshagreened to densely tes-*

sellate, usually with fine reticular shagreening, in one species with abundant long hooked hairs, *less than one and one-half times as long as median clypeal length;* maxillary palpi 4-segmented, fourth shortest, second usually longest. Integument of head, thorax and terga variously sculptured but *mesoscutum usually with large posteromedian area impunctate* and metasomal tergum 1 often with punctures restricted to basal third or less of dorsal surface medially; tegulae, metanotum and propodeum as in *Eumelissodes. Tergum 6 with gradulus with lateral parts lamelliform and often ending abruptly in a short blunt tooth* (in *Eumelissodes* lateral parts of gradulus of tergum 6 absent or cariniform and short); pygidial plate broadly V-shaped with rounded apex to narrowly U-shaped at least apically.

Vestiture variable; without spatuloplumose hairs; tergum 2 with distal pubescent band interrupted medially, often broadly so; scopal hairs weakly to profusely plumose, brown in one species.

Male. Color and structure as in female with the following additions: clypeus pale, yellow to white, never partially or wholly black; base of mandible with yellow to white macula; labrum white, with or without narrow apical dark brown margin; terga with apical margins piceous to translucent brown, never colorless or transparent; *minimum length of first flagellar segment always shorter than half maximum length of second segment and rarely more than one-third of second segment;* terga 6 and 7 with short lateral teeth; pygidial plate notched laterally near apex; *sternum 4, and usually sterna 2, 3 and 5, with apical margin broadly convex, often produced into a more or less hyaline flap and often weakly emarginate medially* (in *Eumelissodes* these sterna not broadly convex but straight or usually broadly concave apically).

Genital capsule as in *Eumelissodes. Sternum 7 with median plate* relatively large, flat (curled laterally over neck of median plate in one species), with abundant short hairs ventrally, *with distinct neck region* (plate proper extends mesally and laterally beyond neck region), *with inner margin of neck smoothly curved, not forming an abrupt angle basally near margin of sternum proper* (as occurs in *Eumelissodes*). Sternum 8 as in *Eumelissodes* but often with apical hairs sparse or absent.

Vestiture as in female except as follows: tergum 2 with distal pale pubescent band usually not or only narrowly interrupted; tergum 5 with pubescent band similar to that of tergum 4; terga 6 and 7 with hairs white to dark brown.

KEY TO THE SPECIES OF THE SUBGENUS CALLIMELISSODES

MALES

1. Sternum 4 with a broad, hyaline, apical flap medially as long as basal part of sternum and feebly emarginate medially; sternum 3 with broad, bilobed, hyaline flap similar to sternum 2 but shorter; sterna 2 and 5 broadly convex and hyaline apically; clypeus white or cream-colored (rarely pale yellow) ..... *stearnsi*

Sternum 4 with apex broadly convex and emarginate medially but not forming a broad hyaline flap; sternum 3 with apical margin convex to almost straight; sterna 2 and 5 with margins weakly convex to straight; clypeus white, cream-colored or yellow 2

2 (1). Genal area laterad of compound eye with round punctures as large as punctures elsewhere on head (except clypeus) and separated mostly by one puncture width or less; vertex between lateral ocelli and apex of compound eye with deep, round punctures separated mostly by less than one puncture width 9

Genal area laterad of compound eye with minute punctures mostly separated by two or more puncture widths; vertex between lateral ocellus and compound eye with small punctures separated by one or more puncture widths 3

3 (2). Flagellar segments 4 through 10 with narrow, shallow, shiny, longitudinal depressions on outer surface, segments 3 and 11 often also with such foveae partly developed 5

Flagellar segments 5 through 10, at most, with narrow depressions on outer surfaces and usually only segments 5 through 9 4

4 (3). Minimum length of first flagellar segment equals more than one-fourth of maximum length of second segment; galeae opaque above, dulled by dense, regular tessellation; flagellar segments without narrow shallow depressions laterally, although there may be shiny flattened areas present, *nigracauda*

Minimum length of first flagellar segment usually equals one-fourth or less of maximum length of second segment; galeae shiny to dull above, but *if* dulled, first flagellar segment equals less than one-fourth second segment; flagellum with at least some segments with narrow, longitudinal, shallow depressions laterally 10

5 (3). Penultimate flagellar segment twice as long as broad or shorter 6

Penultimate flagellar segment more than twice as long as broad 7

6 (5). Galeae opaque, dulled above by dense, coarse, regular tessellation; minimum length of first flagellar segment equals less than one-fifth maximum length of second segment .. 11

Galeae moderately shiny to shiny above, slightly dulled by

delicate reticular shagreening, not tessellate; minimum length of first flagellar segment equals more than one-fifth maximum length of second segment ..... *clarkiae*

7 (5). Terga 2 and 3 with suberect to erect, simple hairs in apical areas; galeae usually shiny and unshagreened or with delicate reticular shagreening; flagellar segment 3 usually with well-developed ventrolateral depression present 12

Terga 2 and 3 with apical areas bare, without simple suberect hairs; galeae often shagreened above; flagellar segment 3 often lacking ventrolateral depression or this depression weak and short 8

8 (7). Terga 2 and 3 with interband zones with abundant, deep, round punctures separated mostly by much less than one puncture width; eyes usually blue or greenish blue, *composita*

Tergum 3, and often tergum 2, with interband zone punctures separated mostly by one puncture width and many by two or three puncture widths; eyes usually green or yellowish green ..... *lustra*

9 (2). Small bees; wing membranes slightly or not at all infumate; tergum 2 with pale pubescent band complete or interrupted medially by no more than one-third width of tergum; penultimate flagellar segment half as broad as long or slightly longer ..... *tuckeri*

FEMALES

1. Galeae above with abundant, long, hooked hairs; terga 2 to 4 covered by short pale pubescence (unless worn); terga 5 and 6 with long hairs dark ochraceous or ochraceous medially to white laterally ..... *stearnsi*

Galeae above with relatively sparse, short, straight hairs; terga 2 to 4 not completely covered by diffuse pale pubescence; terga 5 and 6 with hairs usually dark brown at least medially 2

2 (1). Scopal hairs weakly branched, with one to three branches on each side of rachis ..... *clarkiae*

Scopal hairs profusely branched, with more than three branches on each side of rachis 3

3 (2). Scopal hairs mostly dark brown (occasionally pale brown medially); abdominal vestiture dark brown or black (rarely with slight amount of pale pubescence on tergum 2); galeae densely tessellate ..... *nigracauda*

Scopal hairs white to yellow, brown only near basitibial plate and at apex of basitarsus; galeae variously sculptured ... 4

4 (3). Ultimate flagellar segment as broad as long, truncate ... *lupina*

Ultimate flagellar segment distinctly longer than broad, rounded or obliquely truncate apically 5

5 (4). Large bees, 11 to 16 mm. in length; wing membranes deeply infumate, brown; tergum 2 with short lateral pale pubescent fasciae separated by more than one-third of tergum; pale vestiture yellow-ochre in color ..... *coloradensis*

Small to large bees, 8 to 15 mm. in length; wing membranes hyaline, slightly or not at all infumate; tergum 2 with distal pubescent band often interrupted medially but usually separated by one-third or less of width of tergum; pale vestiture white to ochraceous, rarely rufescent, in color..... 6

6 (5). Integument coarsely punctate, punctures of genal area laterad of compound eye deep, round, separated by less than one puncture width; mesepisterna with crowded, round, almost confluent, deep punctures, surface dulled by fine shagreening ..... *tuckeri*

Integument less coarsely punctate, genal area laterad of compound eye with minute punctures crowded into narrow zone near eye, elsewhere sparse and separated mostly by more than one puncture width..... 7

7 (6). Head with hairs all or mostly black to dark brown; inner surface hind basitarsi and usually tibiae with dark reddish brown to black hairs; galeae above moderately shiny to shiny, unshagreened or with delicate shagreening..*metenua*

Head hairs usually all pale except abundant dark hairs on vertex; inner surface hind basitarsi and tibiae with hairs usually pale, yellow to red; *if* head hairs mostly dark and inner surface hind basitarsi with hairs dark, *then* galeae opaque above, dulled by dense, coarse tessellation..... 8

8 (7). Tergum 1 with crowded punctures restricted to basal third or less medially, middle third, if punctate, with punctures separated mostly by more than two puncture widths; galeae above moderately shiny, often with delicate reticular shagreening but not densely tessellate..... 9

Tergum 1 with crowded punctures at least in basal half medially and often more, middle third of tergum with punctures separated mostly by one puncture width or less at least basally; galeae above moderately shiny with delicate shagreening to densely and regularly tessellate.. 11

9 (8). Inner surface hind basitarsus with dark reddish brown to black hairs; scopal hairs often yellow; terga 5 and 6 with dark brown to black hairs, with or without lateral tufts of white hairs ..... *glenwoodensis*

Inner surface hind basitarsi with hairs yellow to red; scopal hairs white to pale ochraceous; terga 5 and 6 with pale brown to golden hairs medially and with large lateral tufts of white hairs..... 10

10 (9). Mesoscutum with punctures just mesad of parapsidal line deep, separated mostly by half a puncture width or less, usually or mostly larger than scutellar or mesepisternal punctures ..... *composita*

Mesoscutum with punctures just mesad of parapsidal line shallow, separated mostly by more than half a puncture width (many by two or more puncture widths), of irregular size but often or mostly smaller than most scutellar or mesepisternal punctures ..... *lustra*

11 (8). Galeae above moderately shiny, somewhat dulled by delicate reticular shagreening especially in apical half or less, *plumosa*

Galeae above opaque, dulled by dense, coarse, regular tessellation 12

12(11). Inner surface hind basitarsi with hairs dark reddish brown to black; head hairs all or mostly dark brown or at least face below vertex with a few dark hairs mixed with the pale, *ablusa*

Inner surface hind basitarsi with hairs yellow to dark reddish brown; head hairs all white except brown hairs on vertex, face below vertex without dark hairs 13

13(12). Inner surface hind basitarsi with hairs orange; mesoscutal pale hairs dark ochraceous, dark brown patch extends forward beyond transverse line at anterior margins of tegulae, *tribas*

Inner surface hind basitarsi with hairs dark red to dark brown; mesoscutal pale hairs white, dark patch not extending forward to a transverse line at anterior margins of tegulae ..... *minuscula*

Melissodes (Callimelissodes) lupina Cresson

Melissodes lupina Cresson, 1878, Acad. Nat. Sci. Philadelphia, vol. 30, p. 210; Fowler, 1902, Report of the work of the Agric. Exper. Sta. of the Univ. California, 1898-1901, pt. 2, p. 323; Cockerell, 1903, Psyche, vol. 10, p. 77; 1905, Bull. S. California Acad. Sci., vol. 22, p. 305; 1906, Trans. Amer. Ent. Soc., vol. 32, pp. 31, 80; 1906, Trans. Amer. Ent. Soc., vol. 32, p. 309; 1909, Trans. Kansas Acad. Sci., vol. 22, p. 305; Cresson, 1916, Mem. Amer. Ent. Soc., vol. 1, p. 122; Cockerell, 1939, Proc. California Acad. Sci., ser. 4, vol. 23, p. 428; 1939, Bull. S. California Acad. Sci., vol. 38, p. 137; Linsley, 1946, J. Econ. Ent., vol. 39, p. 20; Bohart, Knowlton, Bailey, 1950, Utah State Agric. College Mimeo. series no. 371, p. 5.

Melissodes intermediella catalinensis Cockerell, 1905, Bull. S. California Acad. Sci., vol. 4, p. 102 (new synonymy).

Melissodes humilior catalinensis, Cockerell, 1906, Ann. Mag. Nat. Hist., ser. 7, vol. 17, p. 366.

Melissodes catalinensis, Cockerell, 1923, Proc. California Acad. Sci., ser. 4, vol. 12, p. 86; 1939, Proc. California Acad. Sci., ser. 4, vol. 23, p. 429.

Melissodes catalinensis vanduzeei Cockerell, 1923, Proc. California Acad. Sci., ser. 4, vol. 12, p. 86 (new synonymy).

The females of this species can be distinguished from females of all other species of the genus *Melissodes* by the short apical flagellar segments and by the form of the tibial scopal hairs as described below. The males can be distinguished from other males of the subgenus *Callimelissodes* by the galeae being dulled above, the relatively short first flagellar segment and the lack of a longitudinal sulcus on flagellar segments two through four. In addition, the males have the labrum and mandibular bases yellow and the apical areas of terga 2 to 4 provided with suberect simple hairs.

Female. Measurements and ratios: N, 20; length, 9-13 mm.;

width, 3-4 mm.; wing length, M = 3.23 ± 0.229 mm.; hooks in hamulus, M = 12.20 ± 0.673; flagellar segments 1/segment 2, M = 1.73 ± 0.087.

Structure and color: Integument black; distitarsi and apical half of mandible rufescent; flagellar segments 3-10 (and often apex of segment 2) red to yellow beneath; eyes usually bluish-gray or gray; wing membranes colorless, veins dark brown; tibial spurs yellow to white.

Clypeus with large, shallow, rounded punctures separated mostly by half a puncture width or less, surface dulled by irregular shagreening, without a well-defined boss or median carina apically; supraclypeal area with scattered, deep punctures, surface usually dulled by coarse, reticular shagreening; flattened lateral areas of vertex extending medially and somewhat posterior from apices of compound eyes moderately shiny, dulled by small, round punctures separated by one puncture width or less and by delicate, sparse shagreening; apical flagellar segment as broad as long or broader, truncate; eyes in facial view slightly less than three times as long as wide, converging strongly towards mandibles; maxillary palpal segments in ratio of about 2.4:2.2:2.0:1.0, fourth segment often shorter; galeae with scattered punctures bearing short straight hairs, surface opaque, dulled by dense, regular tessellation. Mesoscutum with punctures round, deep, crowded anteriorly and laterally, but sparse in posteromedian area where separated mostly by two puncture widths and often much more, surface shiny posteromedially but usually dulled anteriorly and laterally by fine shagreening; scutellum with punctures slightly smaller than on adjacent area of mesoscutum and generally more crowded, surface usually dulled by extremely fine shagreening; metanotum with abundant round punctures distinctly smaller than those of mesoscutum, separated mostly by half a puncture width or less, surface opaque, dulled by delicate, fine tessellation; mesepisternum with lateral surface with shallow, round punctures separated mostly by one or less puncture widths, surface dulled by irregular reticular shagreening; propodeum with dorsal surface reticulorugose except medially, posteriorly rugae often assume aspect of discrete large punctures, posterior surface with distinct round punctures separated by one-half to one puncture width except impunctate upper median triangular area, lateral surfaces with crowded punctures, surfaces opaque, dulled by delicate, fine tessellation. Metasomal tergum 1 with basal three-fifths with small, round, shallow punc-

tures crowded basally and laterally, sparser apically except crowded zone at margin of punctate area, apical two-fifths impunctate, surface dulled by dense, reticular shagreening; tergum 2 with basal zone with small, round punctures separated mostly by one puncture width, interband zone with irregular shallow punctures which in lateral raised areas separated mostly by less than one puncture width and medially mostly by two puncture widths, apical zone with minute shallow punctures separated by one to three puncture widths, surface dulled by dense, reticular shagreening; terga 3 and 4 similar, but punctures more crowded in interband zones; pygidial plate V-shaped.

Hair: On head pale ochraceous to white except dark brown on vertex. Thoracic hairs ochraceous to pale ochraceous except as follows: mesoscutum with large dark brown posteromedian patch extending forward usually to a transverse line at anterior margins of tegulae; scutellum with large dark brown median area. Metasomal tergum 1 with long pale ochraceous hairs basally and laterally; tergum 2 with basal zone with long pale ochraceous pubescence, with interband zone with short, suberect, relatively simple, brown to dark ochraceous hairs, with broad, arched, distal, pale pubescent band usually interrupted medially and reaching or almost reaching apex of tergum laterally, with apical area with short, simple, appressed to suberect, brown to ochraceous hairs except narrow glabrous margin; tergum 3 similar to tergum 2 but interband zone often with sparse, appressed, pale pubescence and pale distal pubescent band broader, not interrupted medially and extending to apical margin laterally; tergum 4 with broad apical pale ochraceous pubescent band, occasionally with a few simple, pale hairs near margin medially; terga 5 and 6 with dark brown hairs except lateral pale ochraceous tufts; sternal hairs reddish brown medially to ochraceous laterally. Legs with pale ochraceous to white hairs except as follows: distitarsi usually, basitarsi and inner surfaces of fore tibiae brown, inner surfaces of middle and hind basitarsi dark red to dark brown (usually paler on middle basitarsus), on basitibial plates brown; scopal hairs white to ochraceous, with rachises not extending much beyond plumose part, each hair usually with 4 to 6 branches on each side in apical half or less, with two to several scopal hairs on posterior part of apex of tibia almost sinuous, bent to shape of surface of apical, hairless area of tibia.

Male. Measurements and ratios: N, 20; length, 7.5-11.0 mm.; width, 2.5-4.0 mm.; wing length, $M = 3.12 \pm 0.206$ mm.; hooks in

hamulus, M = 10.95 ± 0.526; flagellar segment 2/segment 1, M = 7.14 ± 0.189.

Structure and color: Integument black except as follows: clypeus, base of mandible and labrum yellow (labrum without dark margin); flagellum yellow to red below (except first segment), dark brown above; eyes gray to bluish gray, rarely greenish blue; wing membranes hyaline, veins brown to black, metasomal terga 2-5 usually opaque, brown, occasionally translucent and yellowish apically; distitarsi rufescent; tibial spurs yellow to white.

Eyes strongly converging towards mandibles, about three-eighths as wide as long; minimum length of first flagellar segment less than one-fifth maximum length of second segment; flagellar segments 5 to 9 with elongate, shiny, shallow, dorsolateral depressions (occasionally also on segment 10 but never on segment 11), penultimate segment more than twice as long as wide, last segment more than three times as long as broad. Maxillary palpal segments in ratio of about 3.25:3.75:2.75:1.0. Apical margin of sternum 4 with broad flap shallowly emarginate medially; sterna 3 and 5 distinctly convex apically. Sculpturing as in female with the following differences: clypeus with punctures coarse and irregular, with surfaces moderately shiny, slightly dulled by sparse coarse shagreening; supraclypeal area with surface usually dulled by dense tessellation; galeae above with coarse shagreening; tergum 1 with basal four-fifths punctate; terga 2-4 with apical areas often with minute punctures (at least a few present near distal pubescent bands).

Sternum 7 with median plate slightly turned laterad, with long, slender neck, with apicolateral angle narrow (almost strap-shaped). Sternum 8 with apicoventral tubercle bidentate apically, with few or no hairs at apex. Gonostylus two-thirds as long as gonocoxite, distinctly capitate, with a few slender hairs on outer and lower surfaces near base; spatha sinuate apically, about three times as wide as long; penis valve with dorsolateral lamella ending at spatha without being turned inward to form a tooth just in front of spatha (Figs. 38-41).

Hair: On head and thorax pale ochraceous to ochraceous, often with brown on vertex of head and usually with a few long brown hairs posteromedially on mesoscutum and almost always on scutellum. Metasomal tergum 1 with basal four-fifths with long pale ochraceous hairs, apically with short, suberect, simple, usually ochraceous, but often pale brown hairs almost to apex; tergum 2 with hairs white to pale ochraceous, basal pubescent band white,

distal pubescent band white and often narrowly interrupted medially, apical area with suberect, simple hairs usually pale ochraceous, but often brown; terga 3 and 4 as in tergum 2 but basal tomentum brown, distal pubescent band not interrupted and apical simple hairs often brown at least medially; tergum 5 as in tergum 4 but distal pubescent band usually reaching margin across entire tergum; terga 6 and 7 ochraceous to pale brown; sternal hairs pale ochraceous, often darkened medially; legs with white to pale ochraceous hairs except as follows: pale rufescent to yellow on inner surfaces of basitarsi and often distitarsi.

Bionomics. This bee is apparently oligolectic upon plants of the family Compositae. Table I summarizes the data leading to this conclusion. Of the 290 collections (787 bees) with flower data attached to the specimens 225 (659 bees) were collections from composites. The remaining 65 collections (128 bees) were collected from plants of 16 families other than composites and, although the numbers of bees are small in the case of each family, the numbers of males usually equal or exceed those of females. This indicates that these families of plants, such as Leguminosae and Polygonaceae, are important to the bees only as nectar sources. Furthermore, Linsley (1946, p. 26) in his study of the pollinators

TABLE II. Summary of Floral Records for *Melissodes lupina*.

Plant Data			Records of *M. lupina*			
FAMILY	Number of genera	Approximate number of species	Number of collections	Number of females	Number of males	Total number of bees
Compositae	28	48	225	436	223	659
Leguminosae	3	4	18	19	22	41
Polygonaceae	2	4	11	17	14	31
Hydrophyllaceae	3	4	8	5	6	11
Brassicaceae	3	3	6	2	6	8
Labiatae	3	3	6	10	4	14
Others (11)	13	13	16	10	13	23
Totals	55	79	290	499	288	787

of alfalfa in California states that *M. lupina* (as well as *M. agilis*) ". . . was rarely encountered or represented by a few males in search of nectar."

Nothing is known concerning the nesting habits of this species. It ranges from high elevations almost to sea level in the western states and is especially abundant in California where it is one of the most abundant species of the genus *Melissodes.*

Type Material. Lectotype male and three male paratypes of *lupina* from California are in the Academy of Natural Sciences of Philadelphia. Holotype female of *catalinensis* from Santa Catalina Island, Davidson collector, is in the University of Colorado Museum at Boulder. Holotype female of *vanduzeei* from Angeles Bay, Gulf of California, June 26, 1921, E. P. Van Duzee collector is in the collection of the California Academy of Sciences, San Francisco (Type No. 946).

Distribution. From Alberta, Canada, in the northeast to Colorado in the southeast, west to southern California and northwest to the state of Washington (Fig. 3). This species has been collected from May 4 until November 8, but mainly from the middle of June until the middle of September. In addition to the type material, 1080 females and 1337 males have been examined from the localities listed below. This list includes localities reported in the literature.

CALIFORNIA: Adobe Creek, Stanislaus Co.; Alameda foothills; Altadena; Antioch; Arroyo Mucho (20 miles S. of Livermore); Artois; Auburn; Avon, Bagby (5.3 miles N. E. of); Bakersfield (15 miles E. of); Bass Lake; Ben Grant Pass; Benica; Berkeley; Berkeley Hills, Alameda Co.; Big Oak Flat, Tuolumne Co.; Big Pine Canyon; Big Rock Creek; Blairsden; Boca Dam (11 miles E. of Truckee); Bolinas; Boquet Canyon (Angeles National Forest); Boulder Creek (4 miles N. W. of); Bridge Creek Camp, Lassen Co.; Bucks Lake, Plumas Co.; Burney (10 miles E. of); Byron; Caliente Mt., San Luis Obispo Co.; Calpine; Calistoga; Cambria Pines, San Luis Obispo Co.; Camp Baldy, Los Angeles Co.; Canby; Capitola; Carbon; Carmel; Carrville; Carson Pass, Alpine Co.; Castle Crags, Shasta Co.; Catalina Island (Fisherman's Cove); Cazadero; Chico; Chile Bar; Clayton; Clovis (4 miles N.); Coalinga; Coffee Canyon, Trinity Co.; Contra Costa Co.; Corral Hollow, San Joaquin Co.; Costa Mesa; Crystal; Cummings; Dales; Davis; Davis Creek, Modoc Co.; Deer Creek, Tehama Co.; Democrat Springs, Kern Co.; Devore; Dixon; Downieville; Dutch Flat, Placer Co.; Eagle Rock; Eagle

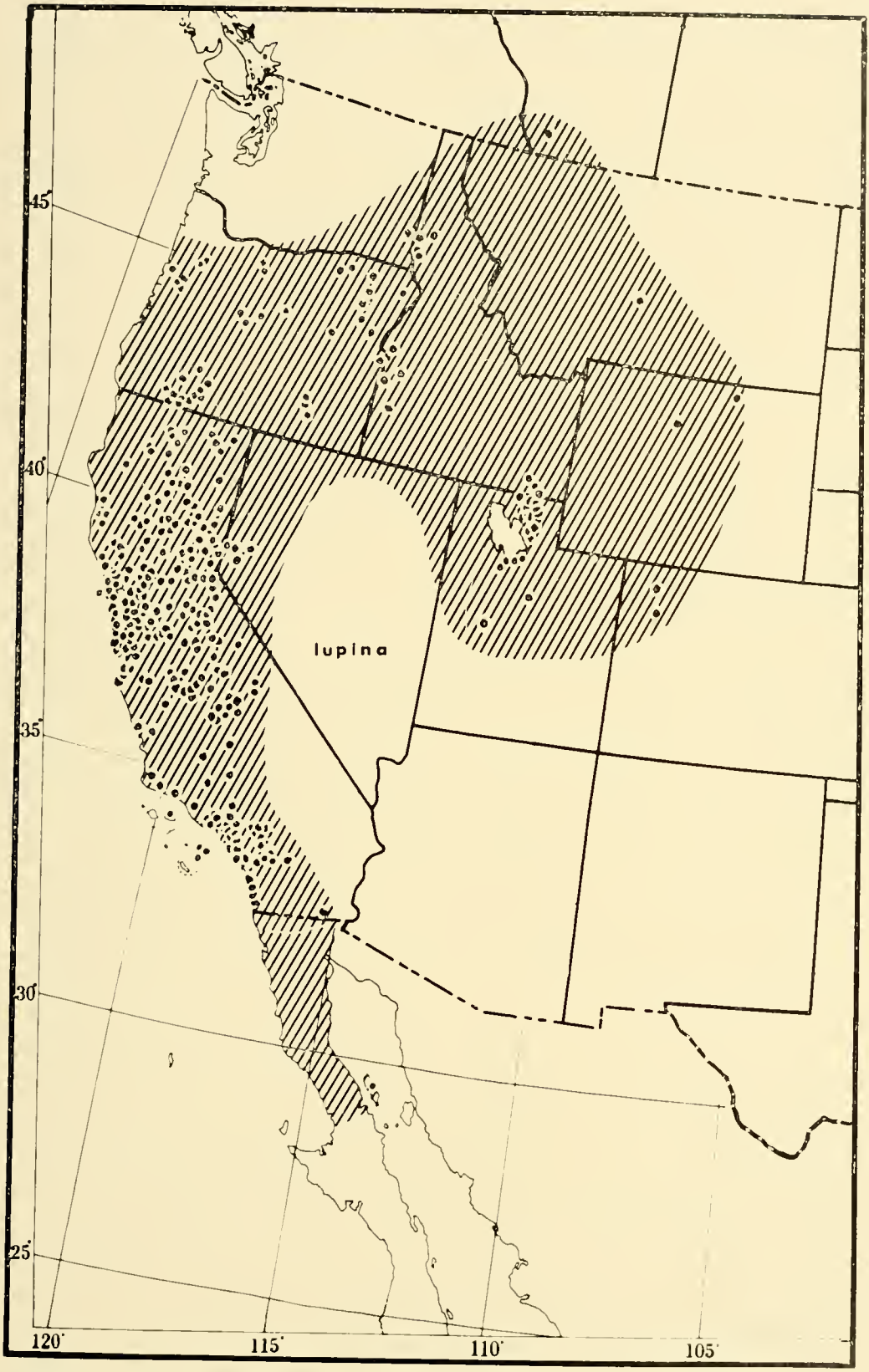

FIG. 3. Map showing the known distribution of *M. (Callimelissodes) lupina* Cresson.

Rock Hills, Los Angeles Co.; Encinitas; Fairfax; Felton; Felton Station, Santa Cruz Co.; Firebaugh; Folsom; Fresno; Friant; Fruto; Galivan; Giant Forest; Glen Blair (mud flats); Glenn Canyon (Santa Cruz Mts.); Guerneville; Harris Spring, Siskiyou Co.; Hemet; Hillsboro; Hobart Mills; Hope Valley, Alpine Co.; Hospital Canyon, Riverside Co.; Huntington Lake; Idyllwild (San Jacinto Mts.); Inverness; Jacksonville; Jamesburg (Hasting's Natural History Reservation); Galivan, Orange Co.; Keddie; Kernville; Knoxville; Kyburz; Laguna Beach; Lagunitas; La Jolla; Lake Almanor, Plumas Co.; Lake Tahoe; Lassen Peak, Shasta Co.; Lebec; Lemon Cove; Linden (10 miles E.); Lindsey; Litchfield; Livermore (13 miles S. of); Loomis; Lower Panoche Creek, Fresno Co.; Lytle Creek, San Bernardino Co.; Madera; Mammoth; Marin Co.; Mariposa, Mariposa Co.; Marsh Creek, Contra Costa Co.; Martinez; Marysville; Mascama Creek, Sonoma Co.; Mason Creek Railroad Siding, Modoc Co.; Maxwell; McCloud; Meadow Valley, Plumas Co.; Mendocina Co.; Mendonta; Merced Falls, Merced Co.; Middletown; Midway Wells; Milbrae; Mill Creek, San Bernardino Co.; Mineral King; Mint Canyon; Mission Valley; Mix Canyon, Solano Co.; Modesto; Mokelumne Hill, Calaveras Co.; Monterey; Monte Rio; Mountain View; Mount Diable, Contra Costa Co.; Mount George, Napa Co.; Mount Harmon, Santa Cruz Co.; Mount Santiago; Mt. Shasta; Murphys, Meyers, Napa Co.; Nelson; Nevada City; Newport Beach; Oak Glen Lodge, San Bernardino Co.; Oakland (hills back of); Oakley; Oceanside; Onion Valley, Plumas Co.; Orinda; Orinda Cross Road, Contra Costa Co.; Oroville; Pacific Grove; Palmdale (Mohave Desert); Palo Alto; Paraiso Springs, Putah Canyon, Yolo Co.; Pasadena; Patterson; Pebbly Beach, Catalina Island; Pinecrest; Pine Knot (Bear Lake); Pinnacles, San Benito Co.; Placerville; Point Reyes, Marin Co.; Pollock Pines, Eldorado Co.; Portola; Puente Hills; Quincy; Raisin City; Red Bluff; Redding; Redwood City; Reseda; Richardson's Spring, Butte Co.; Rio Vista; Riverside; Romoland; Ryan Creek, Mendocina Co.; Sacramento; Sage Hen (near Hobart Mills); Salinas; Samapara; San Antonio Railroad Siding (7 miles S. of), Santa Clara Co.; San Antonio Valley, Santa Clara Co.; San Benito; San Diego; San Fernando; San Francisco; San Mateo; San Mateo Co.; San Ramon; Sonoma Co.; Santa Barbara; Santa Cruz; Santa Cruz Island; Santa Maria (8 miles N. E. of); Santa Monica; Santa Paula; Sargent; Sebastopol; Sequoia National Park (Ash Mt.); Serra; Seven Oaks (San Bernardino Mts.); Shasta Co.; Shaver Lake, Fresno Co.;

Sherman Island; Shingletown; Sierraville; Snowline Camp, Eldorado Co.; Soda Bay (Clear Lake); Squaw Valley, Fresno Co.; Stanford University; Stevens Creek, Santa Clara Co.; Stockton; Strathmore; Strawberry; Strawberry Canyon, Tuolumne Co.; Sutter Buttes, Butte Co.; Tahquitz Valley (San Jacinto Mts.); Tamales Bay (near Marshalls); Tanbark Flat (San Gabriel Mts.); Los Angeles Co.; Termo (3 miles N.); Tesla; Tetley Park (San Bernardino Mts.); Three-Rivers; Tilden Park (San Francisco); Tolay Creek, Sonoma Co.; Tracy; Trimmer; Trinity Co.; Truckee (2 miles N.); Tucker's Grove, Santa Barbara Co.; Tuolumne Co.; Turlock; Twain Harte, Tuolumne Co.; Vallejo; Valley of the Falls; Vincent; Vineburg; Viola; Walnut Creek; Washington; Watts Valley, Fresno Co.; Weber Lake; Weed; West Hollywood Hills; Westley; Westwood Hills, Los Angeles Co.; Whittier; Williams; Willits; Willows; Winters; Wood Lake; Woodland; Yorba Linda; Yosemite; Yosemite Valley. Colorado: Maybell, Meeker. Idaho: Cornell; Coyote Grade, Nez Perce Co.; Cub River Canyon; Downey; Emmett (10 miles E. on Squaw Creek), Gem Co.; Franklin; Grand View; Lewiston; Midvale; Moscow; Parma; Preston. Montana: Winnecook, Wheatland Co. Nevada: Gold Hill, Storey Co.; Reno (Sky Ranch); Verdi; Wadsworth. Oregon: Alsea Mt., Benton Co.; Antelope Mt., Harney Co.; Ashland (12-15 miles E. on Dead Indian Road); Baker; Cayuse; Colestin; Corvallis; Cove; Crater Lake Park; Durkee; Eagle Ridge (Klamath Lake); Elgin (3 miles S. of); Frenchglen; Hereford; Klamath Falls; Kirk (Klamath Marsh); Lake of Woods, Klamath Co.; Maupin; Medford; Mitchell (14 miles E. of); North Powder; Ontario; Pelican Bay, Klamath Co.; Pendleton (9 miles E. of); Prairie City; Prineville; Prospect; Salem; Siskiyou Summit, Jackson Co.; Steen Lake (near Alterson); Steens Mts. (head of Blitzen River); Summitt Prairie; Thomas; Three-Sisters (Dog Camp and Scott Lake); Tigh Valley; Tumalo Reservation, Deschutes Co.; Wallowa National Forest (Lick Creek Railroad Siding); Wood's Creek, Benton Co. Utah: Ballard; Bear River City; College; Collinston; Delta; Erda; Grantsville; Huntsville; Hyrum; Kaysville; Lakespoint; Lewiston; Lincoln; Logan; Mendon; Petersboro; Pineview; Plain City; Portage; Salt Lake City; Smithfield; Thistle; Trenton. Washington: Pullman. Wyoming: Leider; Worland. Alberta: Lethbridge.

Flower Records. Adenostegia pilosa, Adenostoma sp.; *Arctium* sp., *Aster* sp., *A. chilensis, A. exilis, Calchortus nuttalli, Centaurea solstitialis, Centromadia* sp., *C. pungens, Chaenactis artemisiae-*

folia, C. glabriuscula, Chrysopsis villosa, Chrysothamnus sp., *C. nauseosus speciosus, C. v. viscidiflorus, Cirsium* sp., *Cleome serrulata, Coreopsis* sp., *C. lanceolatum, C. tinctoris, Corethrogyne* sp., *C. bernardense, C. filaginifolia, Cosmos* sp., *Croton* sp., *C. californicus, Cryptantha intermedia, Eremocarous setigerus, Ericameria palmeri, Erigeron* sp., *E. foliosus, Eriodictyon* sp., *E. angustifolium, Eriogonum* sp., *E. fasciculatum, E. gracile, E. latifolium, Eriophyllum confertiflorum, Godetia bottae, Grindelia* sp., *G. camporum, G. elata, G. squarrosa, Gutierrezia californica, G. sarothrae, Haplopappus* sp., *H. bloomeri angustatus, Helenium bigelovi, Helianthus* sp., *H. annuus, H. gracilentus, Hemizonia* sp., *H. fasciculata, H. heermannii, H. lobbii, H. luzulaefolia, H. paniculata, H. wrightii, Heterotheca grandiflora, Holodiscus discolor, Iris hartwegi, Ligustrum* sp., *Lotus* sp., *Lythrum* sp., *L. californicum, Mallacothrix* sp., *Marrubium vulgare, Medicago sativa, Melilotus* sp., *M. alba, M. indica, Nemophila* sp., *Perezia microcephala, Phacelia* sp., *P. heterophila, P. humulis, Phalacroseris bolanderi, Pimpinella* sp., *Polygonum auberti, Raphanus* sp., *Rhamnus californica, Salvia* sp., *S. carduacea, Senecio* sp., *Solidago* sp., *S. californica, S. elongata, S. occidentalis, Stephanomeria exigua, S. virgata, Trichostema* sp., *T. laxum, Trifolium repens.*

Melissodes (Callimelissodes) plumosa, n. sp.

This species closely resembles *lupina,* but it probably is more closely related to *metenua.* Both sexes of *plumosa* can be separated from those of *lupina* by the form of the flagella, as described under *lupina.* The females of *plumosa* can be distinguished from those of *metenua* by the paler color of the vestiture, as described below. The males of this species can be distinguished from those of *metenua* only with difficulty. The males of *plumosa* usually have the galeae dulled by delicate tessellation above, and usually have paler and more finely sculptured clypei than those of *metenua.*

Female. Measurements and ratios: N, 19; length, 10-12 mm.; width, 3.5-4.0 mm.; wing length, M = 3.40 ± 0.098 mm.; hooks in hamulus, M = 12.32 ± 0.154; flagellar segment 1/segment 2, M = 2.12 ± 0.034.

Structure and color: Color of integument as in *M. lupina.* Sculpturing and structure as in *lupina* with the following differences: clypeus with punctures averaging slightly smaller, more regularly round in shape, usually with weakly developed median longitudinal carina in apical half, surface moderately shiny, with reticular sha-

greening; supraclypeal area with sparse large punctures, surface shiny, unshagreened or only slightly so; apical flagellar segment longer than broad; maxillary palpal segments in ratio of about 4.6: 3.6:3.6:1.0; galeae with surface dulled by reticular shagreening but moderately shiny. Mesoscutum with posteromedian area often impunctate, surface shiny, not shagreened laterally and anteriorly; surface of scutellum unshagreened; mesepisternum with lateral surface with punctures separated by half or less of one puncture width, surface shiny, with sparse, fine shagreening. Metasomal tergum 1 with basal crowded punctures separated mostly by one puncture width or slightly more; tergum 2 with basal zone with punctures separated mostly by slightly more than one puncture width, apical area with punctures extremely sparse and minute; pygidial plate U-shaped, apical half with sides subparallel, except rounded tip, and diverging only in basal half or less.

Hair: Color of vestiture as in *M. lupina* with the following differences: tergum 4 without simple hairs apicomedially; terga 5 and 6 with brown hairs often much paler than in *lupina,* those of tergum 6 often orange or golden-brown; sternal hairs golden medially to white laterally; legs with hairs of inner surfaces of middle and hind basitarsi and tibiae golden yellow to orange, on basitibial plates pale brown; scopal hairs with rachises not extending much beyond plumose part, usually with 6 or more branches on each side of rachis; apicoposterior tibial scopal hairs usually not sinuate, but occasionally so.

Male. Measurements and ratios: N, 20; length, 9-12 mm.; width, 2.5-4.0 mm.; wing length, $M = 3.17 \pm 0.203$ mm.; hooks in hamulus, $M = 11.15 \pm 0.182$; flagellar segment 2/segment 1, $M = 4.28 \pm 0.099$.

Structure and color: Integumental color as in *M. lupina* except yellow clypeus and base of mandible usually pale yellow and wing veins reddish-brown to brown.

Sculpturing and structure as in *lupina* with the following differences: minimum length of first flagellar segment equals one-fifth or more of maximum length of second segment; penultimate flagellar segments 3 to 10 with shiny, elongate, dorsolateral depressions, and often at base of segment 11 as well; maxillary palpal segments in ratio of about 4.5:3.0:3.0:1.0. Clypeus with crowded, round punctures, in posteromedian area separated by less than one puncture width, surface dulled by reticular shagreening, especially in posterior half; supraclypeal area usually shiny and unshagreened,

or only slightly dulled by shagreening; galeae usually dulled above by fine, reticular shagreening. Metasomal tergum 2 with depressed basal area with small round punctures separated mostly by two puncture widths; tergum 3 with interband zone with punctures separated by less than one puncture width; sternum 4 with apical flap usually not emarginate or only extremely shallowly; sterna 2, 3 and 4 with median impunctate areas usually dulled by dense reticular shagreening.

Sternum 7 with median plate flat, not twisted to face laterally, with apicolateral angle rounded, with short, broad neck, with abundant short hairs ventrally. Sternum 8 usually with one or two hairs apicomedially. Gonostylus less than two-thirds length of gonocoxite, capitate, with sparse short hairs ventrally near base, none laterally; spatha as in *lupina;* penis valve with dorsolateral lamella turned inwards to form a tooth directed medially near spatha (Figs. 42-45).

Hair: Color of vestiture as in *M. lupina* with the following differences: metasomal tergum 2 with distal pale pubescent band often not interrupted medially; terga 3 and 4 with distal pale pubescent bands usually broader than in *lupina.*

Type Material. The holotype female, allotype male, one female and four male paratypes were collected by C. L. Fox at Davis Creek, Modoc County, California, July 13, 1922. Eight additional paratypes were collected by C. L. Fox at Davis Creek, Modoc County, California, as follows: July 14, 1922, 1 female; July 15, 1922, 5 females; July 16, 1922, 2 females. Five additional paratypes were collected by C. L. Fox at Buck Creek, Modoc County, California, as follows: July 21, 1922, 1 female and 3 males; July 25, 1922, 1 female. The holotype and allotype are in the collection of the California Academy of Sciences, San Francisco. Paratypes are in the collections of the California Academy of Sciences, Snow Entomological Museum at the University of Kansas, Lawrence, the U. S. National Museum, and in the author's collection.

Distribution. California, Oregon, Washington and North Dakota (Fig. 4). It is possible that the single male collected in North Dakota is misidentified and should be regarded as *M. metenua* (see the discussion of this below under *metenua*). In addition to the type material listed above, 6 females and 24 males have been examined. The collection data for these are given in full, since relatively few records are involved.

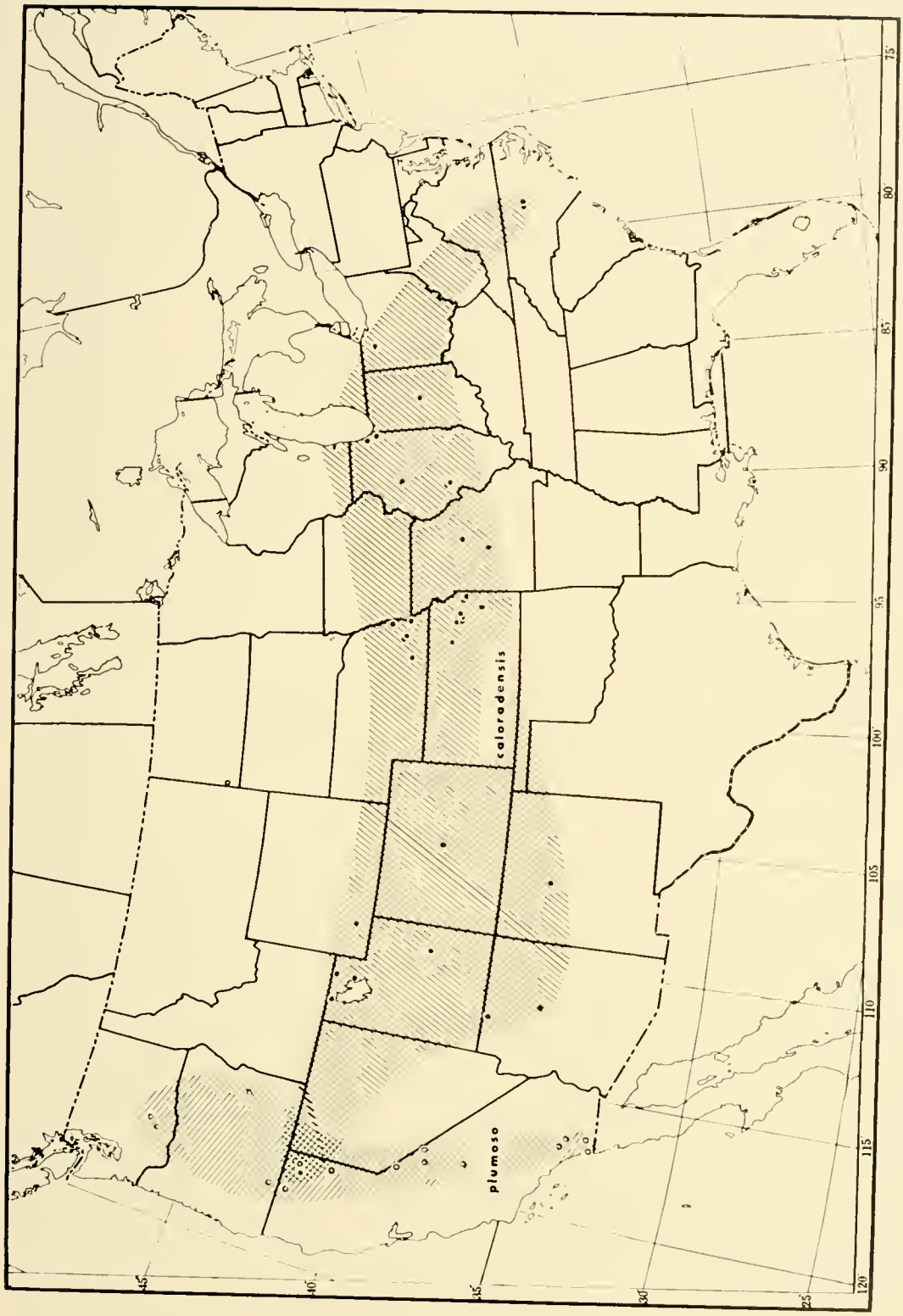

FIG. 4. Map showing the known distributions of *M. (Callimelissodes) plumosa* LaBerge and *M. (C) coloradensis* Cresson.

CALIFORNIA: Anza (2 miles E. of), Riverside Co., 1 female and 1 male on *Encelia californica*, July 7, 1956, E. G. Linsley; Bentons Crossing, Mono Co., 1 male, July 7, 1935, F. R. Platt; Goose Lake, Siskiyou Co., 1 male; Litchfield (22 miles N. of), Lassen Co., 1 male, July 10, 1946, P. D. Hurd and R. F. Smith; Mammoth, Mono Co., 1 male, July 6, 1933, and 1 male, July 8, 1933, G. E. and R. M. Bohart; Pine Valley, 2 females, June 16, 1934, M. T. James; Piñon Flat (4 miles W. of), San Jacinto Mts., 1 female, June 11, 1954, J. C. Hall; San Diego, 1 male, June 24, 1913, W. S. Wright; Sequoia National Park (Ash Mt.), 1 male, June 23, 1951, R. C. Bechtel, 6 males, June 9, 1952, R. C. Bechtel, 1 male, June 9, 1952, R. M. Bohart; Topaz Lake, Mono Co., 1 male, July 17, 1951, A. T. McClay, 2 males, June 26, 1957, J. W. MacSwain. NORTH DAKOTA: Marmarth, 1 male on *Helianthus petiolaris*, July 3, 1949, O. A. Stevens. OREGON: Juntura (Drinkwater Pass), 1 female, July 14, 1940, H. A. Scullen; Klamath Falls, 1 female, July 7, 1934, E. C. VanDyke. WASHINGTON: White Swan (8 miles S. of, on Mt. Adams Highway), Yakima Co., 1 male, August 24, 1941, B. Brookman; Yakima City, 2 males, July 2, 3 and 4, 1882.

Melissodes (Callimelissodes) metenua Cockerell

Melissodes metenua Cockerell, 1924, Pan-Pacific Ent., vol. 1, p. 56.

This is a small dark species closely related to *plumosa* and to *lupina*. The females of *metenua* can be separated from those of *lupina* by their longer ultimate flagellar segment and by the hairs of the head being all or almost all black. The females are distinguished from those of *plumosa* by the darker vestiture, as described below, and by the usually shiny galeae. The males of *metenua* are readily distinguished from those of *lupina* by the form of the flagellar segments, as described below, and by the shiny, usually unshagreened galeae. The males of *metenua* are exceedingly similar to those of *plumosa*. However, in *metenua* the galeae are usually unshagreened and shiny and the clypeus is brighter in color and more coarsely punctate than in *plumosa*.

Female. Measurements and ratios: N, 20; length, 9.0-11.5 mm.; width, 3-4 mm.; wing length, $M = 3.32 \pm 0.149$ mm.; hooks in hamulus, $M = 11.95 \pm 0.114$; flagellar segment 1/segment 2, $M = 1.89 \pm 0.003$.

Structure and color: Integumental color as in *M. lupina* with the following exceptions: eyes grayish green to bluish green; wing membranes slightly infumate, veins dark brown to black; tibial spurs rufescent to yellowish brown.

Sculpturing and structure as in *lupina* with the following differences: clypeal punctures round, separated mostly by less than half a puncture width, surface moderately shiny, somewhat dulled by transverse shagreening, especially posteriorly; supraclypeal area with the surface shiny, unshagreened or sparsely so; vertex with lateral flattened areas at apices of compound eyes shiny, punctures separated mostly by one or more puncture widths; apical flagellar segment distinctly longer than broad, rounded distally, eyes often slightly more than three times as long as broad; maxillary palpal segments in ratio of about 2.3:2.3:2.0:1.0, occasionally with a minute fifth segment; galeae with surface usually shiny and unshagreened or with extremely delicate, reticular shagreening. Mesoscutum with posteromedian area often impunctate, surface not usually dulled by shagreening anteriorly or laterally; scutellum with surface not shagreened; metanotum usually shiny medially; mesepisternum with punctures separated mostly by half a puncture width or less, surface shiny, delicately or not shagreened. Metasomal tergum 1 with basal half punctate, medially separated mostly by more than one puncture width and many by two or more puncture widths; tergum 2 with basal depressed area with round punctures separated by one to two puncture widths, with interband zone punctures small, separated mostly by two puncture widths or more in lateral raised areas, apical area essentially impunctate or with few shallow punctures near pale pubescent band; tergum 3 similar but punctures of basal and interband zones more crowded; pygidial plate narrowly V-shaped with rounded apex.

Hair: Vestiture variable; darkest individuals with hairs all black except scopal hairs pale yellow to whitish on tibia and pale yellow to brown on basitarsus, and outer surface of fore and middle tibiae white apically. The palest specimens are as follows: head hairs all black; thoracic hairs black to dark brown except mesoscutum pale ochraceous on anterior third and at extreme sides, scutellum fringed with pale, metanotum and propodeum above with pale, and mesepisternum with upper third of lateral surface with ochraceous hairs; metasomal tergum 1 with a few pale hairs mixed with the dark in basal half; tergum 2 with narrow lateral oblique fasciae of cinereous pubescence, fasciae separated by at least length of one fascia; tergum 3 with distal pale band of cinereous pubescence not reaching apex of tergum; tergum 4 with apical band of pale pubescence separated from apex in 5 and 6 with hairs all dark; scopal hairs pale yellow to white except brown near basitibial plate and

apically and laterally on basitarsus; fore and middle tibiae often white on outer surface near apex. In individuals between these two extremes pale hairs appear in the following order: first, in the pale fasciae of tergum 3 and on dorsal surface of propodeum and metanotum; second, laterally on tergum 4 and fringing scutellum and anteriorly on mesoscutum; third, on tergum 2, on mesepisterna and on base of tergum 1.

Male. Measurements and ratios: N, 20; length, 8-11 mm.; width, 2.5-3.5 mm.; wing length, M = 3.01 ± 0.182 mm.; hooks in hamulus, M = 11.15 ± 0.150; flagellar segment 2/segment 1, M = 4.39 ± 0.087.

Structure and color: Integumental color as in *M. lupina* with the following exceptions: clypeus usually bright orange-yellow; eyes grayish green to bluish green; wing membranes slightly infumate; tibial spurs yellow to slightly brownish at edges.

Structure as in *M. lupina* with the following differences: eyes more than three-eighths as broad as long; minimum length of first flagellar segment one-fifth or less as long as maximum length of second segment; flagellar segments 3 to 10 and often base of 11 with shiny, longitudinal, dorsolateral depressions, penultimate segment distinctly longer than broad; maxillary palpal segments in ratio of about 3.0:2.8:2.0:1.0, often with minute fifth segment. Apical margin of sternum 4 with flap not emarginate medially or extremely shallowly so. Sculpturing as in *lupina* with the following exceptions: clypeal punctures coarse, especially posteromedially where separated often by one puncture width or more, surface shiny, unshagreened or only slightly so (especially posteriorly); supraclypeal area with unshagreened or only delicately shagreened surface; galeae above shiny, unshagreened or with delicate reticular shagreening; terga 2-4 with apical areas impunctate or with few, scattered, shallow punctures basally near pubescent bands; sterna 2-4 with median impunctate areas shiny to moderately shiny, with delicate reticular shagreening.

Sternum 7 as in *M. plumosa* but hairs on ventral surface shorter and slightly sparser. Sternum 8 and genital capsule essentially as in *M. plumosa* (Figs. 46-49).

Hair: Color of vestiture as in *M. lupina* with the following differences: pale hairs of head and thorax usually dark ochraceous; often vertex of head, mesoscutum and scutellum with brown apices of metasomal terga with suberect, relatively simple hairs usually sparse and usually dark brown.

Type Material. Female holotype collected by E. P. Van Duzee at Colestin, Jackson Co., Oregon, July 30, 1918 (Type No. 1705), is in the collection of the California Academy of Sciences in San Francisco.

Remarks. One male identified as *M. plumosa* from Marmarth, North Dakota, could possibly be a *M. metenua* male. As stated above, the males of *metenua* and *plumosa* are very difficult to distinguish. The male from North Dakota has its galeae dulled by shagreening, thus it is here considered to be a *plumosa* male. However, it is out of the range of *plumosa* as understood from the other specimens, but was collected not far from the range of *metenua.* Also the clypeal punctation seems to be of the *metenua* type more than of the *plumosa* type.

Distribution. California north to Washington, east to Idaho and northwestern Wyoming, and south to northern Utah (Fig. 5). This species has been collected from June 8 until September 15, but mostly during July and August. In addition to the type material, 87 females and 86 males (of which 75 females and 76 males are from Oregon) have been examined from the localities listed below.

California: Coalinga Pass; Copco, Siskiyou Co.; Eureka; Honeydew, Humboldt Co.; Lake City, Modoc Co.; Lassen Peak, Shasta Co.; Scotia. Idaho: Moscow. Oregon: Antelope Mt., Harney Co.; Ashland (20 miles E. of); Baker; Bellfountin; Colestin; Corvallis; Dillard; Eugene; Foster; Grande Ronde River (N. of Imbler), Union Co.: Green Spring Mt. (17 miles W. of Ashland); Hereford; Independence; Lewisburg (5 miles E. of); Medford; Oakridge; Prineville (25 miles E. of); Roseburg; Shedd; Siskiyou Pass, Jackson Co.; Siskiyou Summit, Jackson Co.; Sixes River, Curry Co.; Sulphur Springs, Benton Co.; Summerville; Thomas; Umqua River, Douglas Co.; Unity. Utah: Huntsville; Logan Canyon. Washington: Yakima. Wyoming: Yellowstone National Park.

Flower records. Cosmos sp., *Erigonum* sp., *Melilotus alba.* Only one of the females examined had collection data regarding the flowers it was visiting. This female was visiting *Melilotus alba.* Therefore, no statement regarding flower habits can be made at this time.

Melissodes (Callimelissodes) clarkiae, n. sp.

This distinctive bee is clearly related to the foregoing three species (*lupina, plumosa* and *metenua*), but probably most closely to *plumosa.* The females are as pale in color as *plumosa,* but are

FIG. 5. Map showing the known distributions of *M. (Callimelissodes) metenua* Cockerell, *M. (C.) ablusa* Cockerell, and *M. (C.) minuscula* LaBerge.

readily distinguished from all species of the subgenus *Callimelissodes* by the weakly branched scopal hairs. The males are easily confused with those of either *metenua* or *plumosa*. The males of *clarkiae* are distinguished from those of *lupina* by the longitudinal, dorsolateral depressions of the flagellum being present on segments 3 through 10 and usually 11 as well. They can be separated from the males of *plumosa* and *metenua* by their shorter antennae, and specifically, by the penultimate flagellar segment being no more than twice as long as broad and usually shorter.

Female. Measurements and ratios: N, 7; length, about 11 mm.; width, about 3.5 mm.; wing length, $M = 3.39 \pm 0.197$ mm.; hooks in hamulus, $M = 11.71 \pm 0.286$; flagellar segment 1/segment 2, $M = 2.02 \pm 0.038$.

Structure and color: Integumental color as in *M. lupina*. Sculpturing and structure as in *lupina* with the following differences: clypeus with punctures smaller, round and regular in size, separated mostly by less than half a puncture width, surface dulled especially posteriorly by reticular shagreening, but moderately shiny; supraclypeal area shiny, delicately or not at all shagreened; flattened lateral areas of vertex with minute round punctures separated mostly by one to two puncture widths, surface shagreened; apical flagellar segment distinctly longer than broad, rounded apically; maxillary palpal segments in ratio of about 3.2:3.2:3.4:1.0, palpi longer in total length than in *lupina;* galeae moderately shiny above, dulled by finely reticular shagreening, usually less so in apical third. Mesoscutum not shagreened laterally and anteriorly, usually with small posteromedian impunctate area; metanotum often with dorsomedian area shiny, unshagreened; mesepisternum with lateral surface slightly or not at all shagreened, punctures round, deep, separated mostly by half a puncture width. Metasomal tergum 2 with basal area with minute round punctures separated mostly by more than one puncture width and often by more than two puncture widths, interband zone with punctures separated mostly by one to two puncture widths, not much sparser medially than laterally, apical area impunctate; tergum 3 with narrow apical area impunctate; pygidial plate U-shaped with arms diverging in basal half or less and subparallel apically.

Hair: On head and thorax cinereous except dark brown on vertex, mesoscutum with large posteromedian brown patch extending forward to a line at anterior margins of tegulae or almost so, and scutellum brown medially. Vestiture of metasoma as in *M. lupina*

except as follows: metasomal terga 2 and 3 with apical areas with suberect hairs more abundant; tergum 3 separated from apical margin across all or most of tergum; tergum 4 without suberect simple hairs medially near apical margin; terga 5 and 6 with hairs pale brown except large lateral cinereous tufts; sternal hairs golden brown medially to white laterally. Legs with white or pale ochraceous hairs except as follows: fore basitarsi and often distitarsi and often middle and hind basitarsi dark brown; fore and middle tibiae and middle basitarsi with inner surfaces yellow to red; hind basitarsi and tibiae with inner surfaces yellow to reddish-orange; scopal hairs white except pale brown on and near basitibial plates, with rachises extending far beyond plumose part, with branches sparse, usually one or two on each side of rachis, and long.

Male. Measurements and ratios: N, 10; length, 8-11 mm.; width, 2.0-2.5 mm.; wing length, $M = 2.90 \pm 0.253$ mm.; hooks in hamulus, $M = 10.60 \pm 0.267$; flagellar segment 2/segment 1, (9) $M = 3.46 \pm 0.100$.

Structure and color: Integumental color as in *M. lupina* except as follows: labrum narrowly margined by dark brown; clypeus lemon-yellow with extremely narrow, dark brown posterior zone (darkened especially at posterolateral angles).

Structure and sculpturing as in *lupina* except as follows: eyes slightly less than three-eighths as wide as long; minimum length of first flagellar segment more than one-fifth maximum length of second segment, often ratio equals one-fourth or greater; antennae short, in repose not quite reaching pterostigma; flagellar segments 3 through 10 (and often base of 11) with longitudinal, dorsolateral, shiny depressions; penultimate flagellar segment no longer than twice width and usually slightly less, maxillary palpal segments in ratio of about 5:4:4:1, last segment often shorter; clypeus with punctures round, separated mostly by half a puncture width or less (slightly more posteromedially), surface dulled by reticular shagreening; supraclypeal area usually sparsely shagreened; galeae shiny above with fine reticular shagreening in basal half to two-thirds. Sculpturing of metasomal terga much as in female, but tergum 1 with basal four-fifths punctate; sternum 4 with apical broad flap not, or extremely shallowly, emarginate medially.

Sternum 7 as in *plumosa*, but median plate with fewer hairs ventrally and membranous area below median plate and mesad of inner margin of lateral plate reduced in size. Sternum 8 as in *plumosa* but medioventral tubercle usually not bidentate but

rounded apically, usually with several minute hairs along distal margin. Genital capsule essentially as in *plumosa* but spatha with apical margin usually less sinuate (Figs. 50-53).

Hair: Vestiture as in *M. lupina* except as follows: pale hairs of head and thorax cinereous; vertex usually and mesoscutum often without brown; metasomal terga 6 and 7 with hairs golden-yellow to golden-brown.

Bionomics. In spite of the paucity of data it is apparent that *M. clarkiae* is an oligolectic bee restricted to plants of the family Onagraceae for its pollen. The scopal hairs of the female, each with only two to four long, slender branches, is admirably adapted to

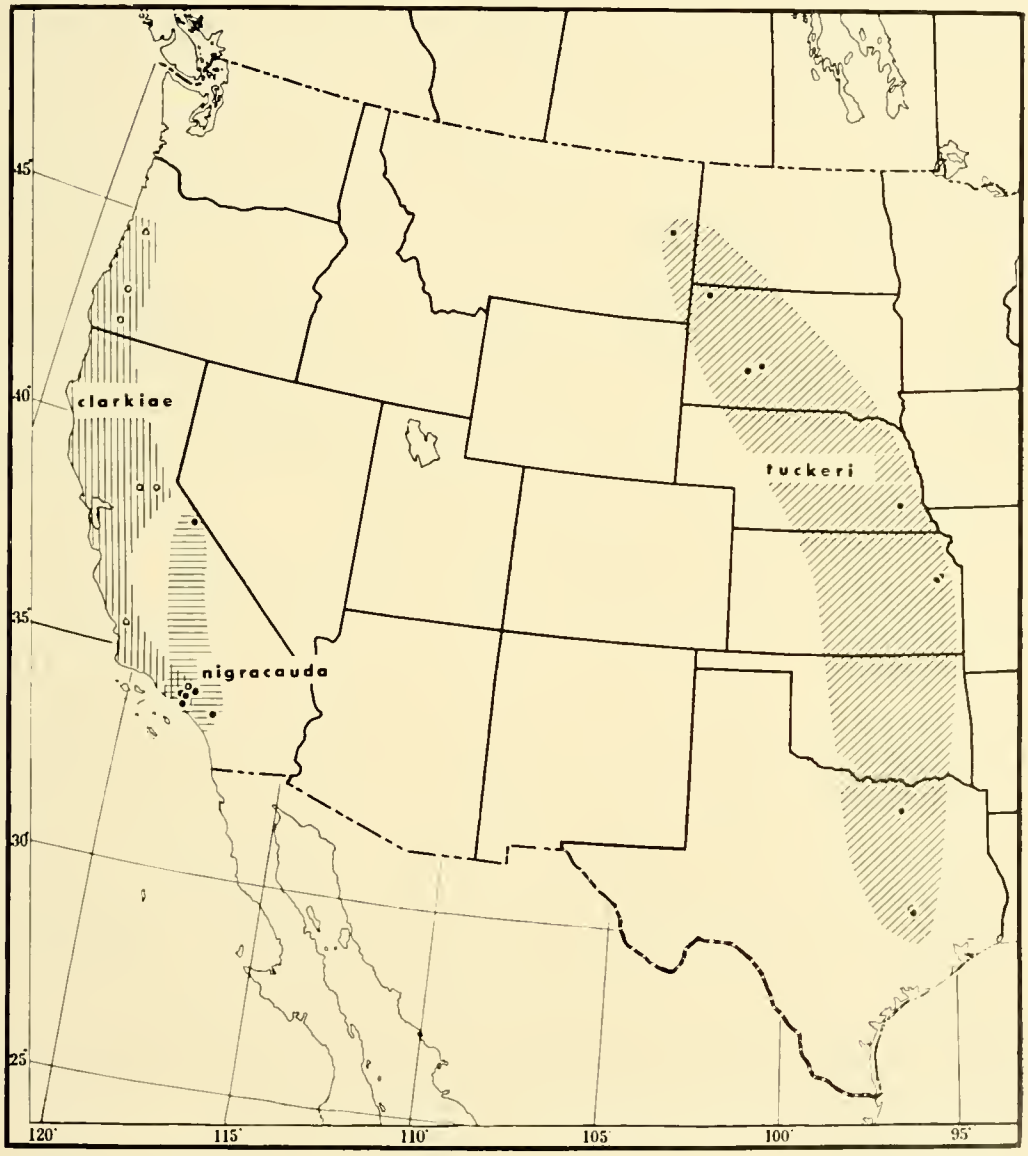

FIG. 6. Map showing the known distributions of *M. (Callimelissodes) clarkiae* LaBerge, *M. (C.) tuckeri* Cockerell, and *M. (C.) nigracauda* LaBerge.

carrying either the cobwebby type of pollen (as in *Oenothera*) or the tetrahedron type (as in *Clarkia* or *Godetia*). It would be difficult to conceive of such scopal hairs as serving to carry the composite pollens or other small, round, dry pollens. Of the seven females available for study the holotype was collected on *Clarkia* and bears its pollen in its scopae, five females bear only *Clarkia*-type (or the tetrahedron) pollen in their scopae and a single female bears the cobwebby type of pollen with a few grains of presumably *Clarkia* pollen intermixed.

Type Material. Holotype female, allotype male and ten male paratypes were collected by E. G. Linsley eight miles west of Atascadero, San Luis Obispo County, California, July 3, 1956, on *Clarkia speciosa speciosa.* In addition 6 females and 2 male paratypes are as follows: CALIFORNIA: Folsom, 1 female, May 30, 1952, T. R. Haig; Snowline Camp, Eldorado Co., 1 male, July 20, 1948, P. D. Hurd; Tanbark Flat, Los Angeles Co., 2 females, July 14, 1950, W. C. Bentinck. OREGON: Corvallis, 1 female and 1 male, July 19, 1933, Joe Schuh; Grants Pass, 1 female, July 12, 1935; Roseburg, 1 female, June 28, 1925 (distribution map, Fig. 6). The holotype and allotype are in the collection of the University of California at Berkeley. Paratypes are in the collections of the University of California at Berkeley, Oregon State College at Corvallis, the Snow Entomological Museum of the University of Kansas at Lawrence, Dr. J. G. Rozen and in the author's collection.

Melissodes (Callimelissodes) ablusa Cockerell

Melissodes metenua ablusa Cockerell, 1926, Pan-Pacific Ent., vol. 3, p. 85.

This species is closely related to the preceding four species and most closely resembles *metenua* in the dark color of the vestiture. The females of *ablusa* can be separated from those of *metenua* and *plumosa* by the densely tessellate galeae, the more densely punctate metasomal terga, the small size and the usual dark hair color. The males of *ablusa* are like those of *clarkiae* in that flagellar segments 4 to 10, and often 3 and 11, have the dorsolateral, longitudinal depressions and the penultimate flagellar segment is no more than twice as long as wide. The males of *ablusa* can be separated from those of *clarkiae* by the densely and regularly tessellate galeae and by the sculpturing of the terga as described below.

Cockerell did not have the male of this species when he first proposed the name. The male described below was not collected with any females and is considered to be the male of *ablusa* on the

basis of structure and color. This association of sexes is, therefore, provisional.

Female. Measurements and ratios: N, 9; length, 9-11 mm.; width, 3.5-4.0 mm.; wing length, M = 2.73 ± 0.199 mm.; hooks in hamulus, M = 11.22 ± 0.223; flagellar segment 1/segment 2, M = 2.12 ± 0.042.

Structure and color: Integument as in *lupina* except eyes green to yellowish green, wing membranes slightly infumate and tibial spurs yellow to reddish brown. Structure and sculpturing as in *lupina* except as follows: clypeus with punctures crowded, small, regularly round, separated by less than half a puncture width except at extreme base medially; supraclypeal area shiny, unshagreened; flattened areas of vertex near apices of compound eyes with small round punctures separated mostly by less than half a puncture width; apical flagellar segment distinctly longer than broad, rounded distally; maxillary palpal segments in ratio of about 6:5:5:1; galeae narrow, surface opaque, dulled by dense, regular coarse tessellation. Mesoscutum with large posteromedian area impunctate (area about one-third of total surface), punctures surrounding impunctate area small; scutellum with punctures sparse medially, separated mostly by more than one puncture width; metanotum shiny medially; mesepisternum with lateral surface with punctures smaller than mesoscutal punctures, crowded, separated by half a puncture width or less, surface moderately shiny to dull, shagreened. Metasomal tergum 1 with basal half with crowded, shallow punctures, surface shiny to moderately so, with extremely fine reticulotransverse shagreening; tergum 2 with interband zone with deep, round, regular punctures separated by one-half to one puncture width, apical area with abundant, deep, round punctures separated mostly by one-half to one puncture width except narrow apical impunctate area, surface shiny, with extremely fine reticulotransverse shagreening; tergum 3 and 4 similar to tergum 2 but apical area obliterated or almost so by distal pubescent area; pygidial plate narrow, U-shaped, sides subparallel in apical half.

Hair: Darkest specimen as follows: head all black; thorax dark brown except sparse pale brown to ochraceous hairs surrounding wing base and dorsally on metanotum and propodeum; metasoma all dark brown except tergum 2 with basal zone with pubescence ochraceous, with broad, lateral oblique fasciae of pale pubescence (fasciae may almost meet medially and may reach apical margin

laterally but, if so, dark brown medially and apicolaterally), tergum 3 with distal pale pubescent band interrupted medially by brown pubescence and separated from apical margin across entire tergum by dark brown pubescence and suberect hairs, tergum 4 with apical pale pubescent band dark brown (or pale brown laterally only); terga 5 and 6 without pale hairs laterally; leg hairs dark brown except scopal hairs yellowish white. Palest specimens as in *M. lupina* except as follows: face except clypeus dark brown mixed with pale ochraceous (brown especially along inner margins of eyes, surrounding antennal fossa and surrounding supraclypeal area); metasomal terga 2 and 3 with distal pale bands narrowly interrupted medially; tergum 4 with median third with narrow dark brown pubescent area along apical margin and with scattered brown pubescence in pale band basal to this; tergum 5 with small lateral pale tufts; sternal hairs brown except at extreme apical margins of sterna 3 to 5 and at extreme sides; coxae, trochanters and femora brown, hind tibiae and basitarsi with inner surfaces dark brown, fore and middle tibiae and tarsi dark brown except outer apical surfaces of tibiae. Intermediate specimens mostly similar to darkest form; pale color progresses as described for *M. metenua* except head usually with more pale present and darkens concurrently with thorax.

Male. Measurements and ratios: N, 1; length, about 10 mm.; width, about 3 mm.; wing length, 5.19 mm.; hooks in hamulus, 11; flagellar segment 2/segment 1, 4.57.

Structure and color: Integumental color as in *M. lupina* except as follows: clypeus and mandibular base cream-colored, almost as pale as labrum; eyes gray. Structure as in *M. lupina* except as follows: flagellar segments 3 to 10 and base of 11 with ventrolateral, shiny, longitudinal depressions, penultimate segment twice as long as wide, ultimate segment much less than three times as long as wide; maxillary palpal segments in ratio of 2.2:2.0:2.0:1.0. Apical margin of sternum 4 not emarginate medially. Sculpturing as in female except as follows: clypeal punctures slightly coarser and more widely spaced: mesepisternum with lateral surface shiny, only sparsely shagreened; metasomal tergum 1 with basal four-fifths densely and regularly punctate; terga 2 to 4 with apical areas not punctate.

Sternum 7 as in *M. plumosa* but membranous area between inner edge of lateral plate and lower part of median plate almost obliterated, linear. Sternum 8 as in *plumosa* but apicoventral tubercle not bidentate, rounded apically and slightly surpassing apical margin

medially, without median apical hairs. Genital capsule as in *M. plumosa.*

Hair: Vestiture of head and thorax pale ochraceous (yellowish on dorsum of thorax) except sparse brown hairs medially on scutellum. Metasomal vestiture as in *M. lupina* except as follows: terga 1-3 without short brown hairs apically; tergum 2 with suberect hairs of interband zone ochraceous; terga 2 and 3 with apical areas glabrous; terga 4 and 5 with distal pale bands continuous, reaching apical margin except medially; terga 6 and 7 with dark brown hairs.

Remarks. As stated in the diagnosis, the male described here is provisionally associated with this species. It is similar to the females in regard to the sculpturing of the galeae, clypeus, mesoscutum, scutellum and metasoma. However, this male is extremely similar to the male of the next species described below which is very closely related to *M. ablusa,* according to the structural characters of the females.

Type Material. Holotype female collected by E. C. Van Dyke at Millbrae, California, September 1, 1912. Cockerell (1926) mentions seven female paratypes collected with the holotype, but I have been able to see only three of these paratypes. Also examined were six additional females collected with the holotype, but not recorded by Cockerell, one female collected by E. C. Van Dyke at Millbrae on October 3, 1926, and one male collected by R. M. Bohart, July 23, 1953, at Bolinas, California (see Fig. 5 for distribution map). The holotype is in the collection of the California Academy of Sciences in San Francisco. Paratypes are in the collections of P. H. Timberlake at the Citrus Experiment Station in Riverside, California, and in the U. S. National Museum. The single male described above is in the collection of the University of California at Davis.

Melissodes (Callimelissodes) minuscula n. sp.

This small species is closely related to *M. ablusa* Cockerell and perhaps is only a color variety of the latter. However, *minuscula* is relatively uniform in color and does not show evidence of grading toward the darker *ablusa.* Furthermore, *minuscula* shows some differences from *ablusa* in sculpturing, as described below. Both sexes of *minuscula* can be distinguished from the other members of the subgenus *Callimelissodes* in the same manner as *M. ablusa* except for the pale vestiture of *minuscula.*

Female. Measurements and ratios: N, 20; length, 9-10 mm.; width, 2.5-3.5 mm.; wing length, M = 2.50 ± 0.085 mm.; hooks in hamulus, M = 11.20 ± 0.186; flagellar segment 1/segment 2, M = 2.15 ± 0.026.

Structure and color: Integumental color as in *lupina.* Structure and sculpturing as in *ablusa* except as follows: clypeus often with an indistinct longitudinal median carina; maxillary palpal segments in ratio of about 7:5:4:1, last segment often slightly longer; galeae tessellate as in *ablusa;* mesoscutal punctures surrounding impunctate posteromedian area large and deep, between impunctate area and parapsidal line separated mostly by one-half to one puncture width; mesepisternum with punctures as large as mesoscutal punctures, separated mostly by less than half a puncture width, surface shiny, unshagreened; metasomal tergum 2 with apical area impunctate except medially where pubescent band is interrupted, here punctures large, shallow, separated mostly by one to two puncture widths, surface moderately shiny; tergum 3 with interband zone with dense, regular, round punctures separated by less than half a puncture width; pygidial plate narrowly U-shaped, sides subparallel in apical third, occasionally narrowly V-shaped when worn.

Hair: Vestiture uniformly white except as follows: vertex with abundant dark brown; mesoscutal pale hairs pale ochraceous, dark patch not extending forward beyond a transverse line at about middle of tegulae; scutellum with sparse dark brown hairs medially; metasomal tergum 1 pale ochraceous in basal half, with sparse, simple, dark brown, minute, appressed hairs apically; tergum 2 with interband zone with brown suberect hairs at least medially, with pale distal pubescent band broad, reaching apical margin laterally, narrowly interrupted medially; tergum 3 with interband zone with diffuse white pubescence, basal zone with dark brown tomentum, distal pale band uninterrupted, reaching apical margin across most or all of tergum; tergum 4 dark brown basally, distal white pubescent band uninterrupted apicomedially; terga 5 and 6 with pale brown to orange hairs (paler on tergum 6) medially and with large lateral white tufts equalling one-fourth to one-third of width of tergum; sternal hairs yellowish to brown medially; legs with dark brown to reddish brown hairs on fore tarsi and inner surfaces of hind basitarsi; scopal hairs highly plumose.

Male. Measurements and ratios: N, 10; length, 7-10 mm.; width, 2-3 mm.; wing length, M = 2.36 ± 0.219 mm.; hooks in hamulus, M = 10.30 ± 0.300; flagellar segment 2/segment 1, (9) M = 4.26 ± 0.139.

Structure and color: Integumental color as in *M. lupina* except as follows: clypeus and mandibular base pale yellow to cream-colored; flagellum yellow below to dark red above; wing veins red to reddish brown. Structure as in *M. lupina* except as follows: eyes slightly more than three-eighths as broad as long; flagellar segments 3 to 10 and base of 11 with shiny, longitudinal, dorsolateral depressions, ultimate segment less than three times as long as board, penultimate segment twice as long as broad or shorter; maxillary palpal ratio about 3.5:2.5:2.5:1.0. Apical margin of sternum 4 not emarginate medially or only extremely shallowly so. Sculpturing as in female with the following differences: supraclypeal area often dulled by sparse reticular shagreening; mesoscutum with postero-median impunctate area reduced or absent; metasomal tergum 1 with coarse punctures almost to apical margin medially but sparse in median third where punctures separated by 2 to 3 puncture widths; terga 2 and 3 with narrow apubescent apical areas (if present) impunctate.

Sternum 7 as in *M. plumosa* but membranous area between inner margin of lateral plate and base of median plate almost obliterated, linear. Sternum 8 as in *plumosa* but apicoventral tubercle rounded, not bidentate, and surpassing margin of sternum medially; with a few apicomedial hairs. Genital capsule as in *M. plumosa.*

Hair: Hair and pubescence pale ochraceous except as follows: yellowish ochraceous on vertex of head, mesoscutum and scutellum; metasomal terga 3-5 with tomentum at extreme base dark brown; tergum 2 with pale distal band reaching apical margin at least at sides, uninterrupted medially; terga 3 and 4 with pale distal bands reaching apical margins at least in lateral thirds, with diffuse pale pubescence in interband zones; terga 6 and 7 ochraceous to golden brown; basitarsi and distitarsi with inner surfaces yellow to red (red especially on fore and middle basitarsi).

Type Material. Holotype female, allotype male and 10 female paratypes were collected by R. R. Snelling near the San Joaquin River, 10 miles S. W. of Turlock, Stanislaus County, California, on July 13, 1952. Additional paratypes include 17 females and 9 males from California as follows: Avon, Contra Costa County: 3 males, August 29, 1937, E. C. Van Dyke. Bakersfield, Kern County: 1 male, July 24, 1929, R. H. Beamer. Kaweah, Tulare County: 1 male, June 19, 1936, F. T. Scott. Kern County: 1 male, June 19, 1936, F. T. Scott. Ridge Route, Los Angeles County: 1 male, June 13, 1931, H. A. Scullen. Tracy, San Joaquin County: 2 males, June

21, 1949, Ray F. Smith. Turlock (10 miles S. W. of, near San Joaquin River): 2 females, July 31, 1952, R. R. Snelling; 1 female on *Cressa cretica,* August 6, 1951, R. R. Snelling; 5 females on *Cressa cretica,* July 28, 1953, R. R. Snelling; 7 females on *Heliotropum curassavicum,* August 6, 1951, R. R. Snelling; 2 females, August 6, 1951, R. R. Snelling (distribution map, Fig. 5).

The holotype and allotype are in the collection of the California Academy of Science at San Francisco. Paratypes are in the collections of R. R. Snelling, Turlock, California, the Snow Entomological Museum of the University of Kansas, Lawrence, P. H. Timberlake of the Citrus Experiment Station, Riverside, California, the University of California at Berkeley, the California Academy of Sciences at San Francisco, Oregon State College at Corvallis and in the author's collection.

Melissodes (Callimelissodes) tribas, n. sp.

M. tribas is a small species known from a single female from San Diego, California. It is closely related to *M. minuscula* which it resembles in color and to *M. ablusa. M. tribas* can be distinguished from *ablusa* by its paler vestiture and from *minuscula* by its larger size, pale hairs of the inner surfaces of the hind basitarsi, and darker thoracic hairs.

Female. Measurements and ratios: N, 1; length, about 9.5 mm.; width, about 3.5 mm.; wing length, 2.92 mm.; hooks in hamulus, 13; flagellar segment 1/segment 2, 2.00.

Structure and color: Integumental color as in *lupina* but eyes gray-green. Structure and sculpture as in *minuscula* except as follows: clypeus without apicomedian carina; maxillary palpal ratio about 2.7:1.3:1.3:1.0; galeae tessellate as in *ablusa;* mesoscutal punctures surrounding posteromedian impunctate area large, deep, surface shiny; tergum 1 with basal three-fifths with deep, round punctures separated mostly by half a puncture width; tergum 2 with apical area absent, surface beneath apical pubescent band with small, round punctures separated by two to three puncture widths; pygidial plate U-shaped in apical half, narrow, sides diverging basad.

Hair: Vestiture as in *minuscula* except as follows: mesoscutal pale hairs dark ochraceous, dark brown posteromedian patch rounded, twice area of scutellar dark patch or slightly more, extending forward beyond a transverse line at anterior margins of tegulae; tegulae without brown; metasomal tergum 2 with distal pale band uninterrupted, apical, interband zone with some short,

suberect, brown, simple hairs at least medially; tergum 5 brown basally, yellow-orange apicomedially, white laterally; tergum 6 orange medially to white laterally; sternal hairs yellow medially, white laterally; inner surfaces hind basitarsi orange; scopae white.

Type Material. The holotype female from San Diego, California, June 5, 1913, is in the collection of Cornell University, Ithaca, New York.

Melissodes (Callimelissodes) nigracauda, n. sp.

This strikingly colored bee is very distinct and not closely related to any other of the species of this subgenus. It resembles *M. ablusa* and *M. minuscula* in the sculpturing of the galeae in both sexes and in the color of the male clypeus. The females are readily recognized by the vestiture of the head, abdomen and sides of the thorax being dark brown to black, whereas the dorsum of the thorax is ochraceous to slightly rufescent. In addition, the scopal hairs are dark brown to black. The males can be separated from males of other species of the subgenus by the long first flagellar segment and by the flattened condition of the flagellar segments as described below. In addition the terminalia are highly distinctive.

Female. Measurements and ratios: N, 20; length, 11-13 mm.; width, 3.5-4.5 mm.; wing length, M = 3.86 ± 0.102 mm.; hooks in hamulus, M = 14.20 ± 0.275; flagellar segment 1/segment 2, M = 2.24 ± 0.241.

Structure and color: Integument black except as follows: flagellar segments 4 (and often 3) to 10, distitarsi, apical half of mandibles and often hind and middle tibial spurs (black in holotype) rufescent; wing membranes infumate, brown. Clypeus with round punctures somewhat elongate apicomedially, separated mostly by one-half to one puncture width, surface moderately shiny, with sparse cross-striations; supraclypeal area shiny, unshagreened or sparsely so; galeae dulled by dense, coarse, regular tessellation; maxillary palpal segments in ratio of about 9:9:8:1, last segment often slightly longer; eyes more than three times as long as broad; vertex with flattened area apicomesad of compound eyes with small round punctures separated by less than one puncture width, surface shiny; ultimate flagellar segment longer than broad. Mesoscutum with small round deep punctures separated mostly by one puncture width at level of parapsidal lines, more crowded anteriorly and lateral to parapsidal lines, sparser in posteromedial area, surface shiny, unshagreened; scutellum punctate as on mesoscutum at level of parapsidal lines, unshagreened; metanotum with

round punctures smaller than on scutellum and separated by less than one puncture width, shiny and sparsely shagreened at least dorsally; propodeum much as in *M. lupina*, but surface moderately shiny, shagreening delicate; mesepisternum with lateral surface with regular round punctures slightly smaller than those of posteromedian area of mesoscutum and separated by one-half to one puncture width, surface unshagreened. Metasomal tergum 1 with basal half with punctures sparse, extremely shallow and indistinct, apical half impunctate, surface dulled by fine, dense, reticulotransverse shagreening, moderately shiny; tergum 2 with basal zone punctures minute, separated by three to four puncture widths, interband zone with indistinct, sparse punctures, apical area impunctate, surface shiny (basal zone) to moderately shiny, shagreened as in tergum 1; terga 3 and 4 as in tergum 2; pygidial plate broadly V-shaped, apex quite pointed.

Hair: Head dark brown to black, occasionally a few pale hairs on vertex and near antennal fossae; thorax with mesoscutum, scutellum, tegulae and dorsal surface of propodeum ochraceous to slightly rufescent, remainder dark brown to black; abdomen dark brown to black except as follows: metasomal tergum 1 often with long pale hairs mixed with dark in basal half (a few pale in holotype); terga 2 and 3 with apical areas with minute, simple, closely appressed, sparse, dark brown hairs; tergum 3 with distal pubescent band often ochraceous in lateral thirds or less (dark brown in holotype); legs with hairs dark brown to black except scopal hairs of tibiae brown to dark brown medially (in holotype basitarsi and tibiae with brown hairs).

Male. Measurements and ratios: N, 20; length, 11-14 mm.; width, 2.5-4.0 mm.; wing length, $M = 3.74 \pm 0.208$ mm.; hooks in hamulus, $M = 12.90 \pm 0.204$; flagellar segment 2/segment 1, $M = 3.27 \pm 0.042$.

Structure and color: Integument black except as follows: clypeus and base of mandible pale yellow to cream-colored; labrum white with narrow apical margin of brown; eyes gray to bluish gray; flagellum except first segment yellow to red below; wing membranes slightly infumate, yellowish, veins dark reddish brown to black; tibial spurs yellow to yellowish brown.

Minimum length of first flagellar segment equals one-fourth or more of maximum length of second segment, ultimate and penultimate segments at least three times as long as broad, flagellum with dorsolateral depressions absent, but shiny areas present on seg-

ments 5 through 11 (and often at base of 4) and these segments distinctly compressed. Maxillary palpal segments in ratio of about 2.50:5.00:2.75:1.00. Sculpturing as in female but metasomal tergum 1 with basal two-thirds to three-fourths punctate and terga 4 and 5 similar to tergum 3. Sternum 4 with apical margin broadly convex and often with extremely shallow emargination medially; sterna 3 and 5 with margins convex, but only slightly so and not apparent if abdomen telescoped.

Sternum 7 with median plate about twice as broad as long, supported by narrow neck at least as long as plate, plate with minute hairs covering all of ventral surface, neck with sparse longer hairs; lateral plate with pronounced proximolateral angle; membranous area small. Sternum 8 with apex truncate, scarcely if at all emarginate medially; ventral tubercle pointed, with minute notch at apex, reaching or slightly surpassing apical margin of sternum. Gonostylus longer than one-half of length of gonocoxite, club-shaped in dorsal view, flattened, apical fourth broader than basal fourth, with minute pointed spicules near base ventrally; gonocoxite with spicules on inner surface at apex (just proximad of gonostylus) mostly long, thick, obtuse; penis valve with dorsal lamella ending anteriorly near spatha in inturned angle or tooth; spatha about 3 times as wide as long, apical margin sinuate (Figs. 54-57).

Hair: Head and thorax ochraceous (slightly darker on mesoscutum and scutellum). Abdomen ochraceous except as follows: tergum 1 with apical area with short, dark brown, appressed hairs; terga 2 to 4, and often medially on 5, with apical areas with short, appressed to subappressed, dark brown, simple hairs; terga 3 to 5 with basal zones with dark brown tomentum; sterna with brown to yellow hairs medially, pale ochraceous laterally. Leg hairs ochraceous except inner surfaces of tarsi golden yellow to orange.

Type Material. Holotype female, allotype male, and thirteen female and three male paratypes were collected by C. D. Michener on *Stephanomeria* sp. at Altadena, California, on September 28, 1935. Seven female and fourteen male paratypes in addition were collected by C. D. Michener at Altadena, California, as follows: 1 male on *Senecio douglasii*, August 2, 1934; 4 females and 12 males on *Stephanomeria* sp., September 13, 1934; 1 female and 1 male on *Stephanomeria* sp., September 30, 1934; 1 female on *Stephanomeria virgata*, August 19, 1935; 1 female on S. *virgata*, August 29, 1935. In addition 10 female and 3 male paratypes were collected in California as follows: Alcalde (Diablo Mt.), 1 female, August 6, 1927;

Boquet Canyon, Angeles National Forest, 1 male on *Erigeron* sp., August 23, 1954, R. R. Snelling; Hot Creek, Mono County, 1 female, July 17, 1953, R. M. Bohart; Pasadena, 3 females and 1 male on *Stephanomeria* sp., September 11, 1934, C. D. Michener; Redondo Beach, Los Angeles County, 1 male, July 20, 1937; Riverside, all on *Stephanomeria exigua* by P. H. Timberlake: 1 female on September 20, 1932, 2 females on September 1, 1933, 1 female on September 12, 1933, and 1 female on September 18, 1933. The holotype and allotype are in the Snow Entomological Museum at the University of Kansas, Lawrence (distribution map, Fig. 6). Paratypes are in the collection of the Snow Entomological Museum, the University of California at Davis, P. H. Timberlake at the Citrus Experiment Station, Riverside, California, R. R. Snelling of Turlock, California, Cornell University, Ithaca, N. Y., the U. S. National Museum, and in the author's collection.

Remarks. It seems likely that this species is restricted to plants of the genus *Stephanomeria* (Compositae) for sources of pollen. However, the data are as yet too sparse to come to a firm conclusion regarding oligolecty. It is perhaps significant that the only other plants from which *nigracauda* has been collected are also composites (*Erigeron* and *Senecio*).

Melissodes (Callimelissodes) composita Tucker

Melissodes lupina var. *composita* Tucker, 1909, Trans. Kansas Acad. Sci., vol. 22, p. 281.

Melissodes lupina, Cockerell, 1909, Trans. Kansas Acad. Sci., vol. 22, p. 305 (misidentification).

Among the foregoing species, *M. composita* is most closely related to *M. plumosa* and *M. metenua.* Both sexes can be distinguished by their relatively shiny galeae, coarsely punctate mesoscutum and scutellum and highly shiny and glabrous apical areas of the terga. The females are distinctive in that the first metasomal tergum has the basal punctures crowded in the basal third or less and absent or scattered apical to this and the second tergum with the interband zone with only scattered punctures medially. The males are distinctive in that the metasomal terga 2 to 4 have the apical areas glabrous and shiny, the antennae as in *M. plumosa*, but the third segment lacks the dorsolateral depression, and coarse punctation on the mesoscutum as described below.

Female. Measurements and ratios: N, 20; length, 9.5-11.0 mm.; width, 3.0-4.5 mm.; wing length, $M = 3.43 \pm 0.118$ mm.; hooks in

hamulus, M = 12.40 ± 0.161; flagellar segment 1/segment 2, M = 1.94 ± 0.025.

Structure and color: Integumental color as in *M. lupina.* Structure and sculpturing as in *lupina* except as follows: clypeus and supraclypeal area with surfaces shiny, with extremely sparse shagreening if any; flattened areas of vertex posteromesad of compound eyes with sparse, minute punctures separated by two to four puncture widths, surface shiny to moderately so, dulled by distinctly reticular shagreening; apical flagellar segment longer than broad; maxillary palpal segments in ratio of about 4:3:3:1; galeae above with surface shiny to moderately shiny, with reticular, delicate shagreening at least in apical half; mesoscutum with large coarse punctures, in area mesad of parapsidal lines separated mostly by less than half a puncture width and larger than scutellar or mesepisternal punctures, laterad of parapsidal lines slightly smaller and separated by less than half a puncture width, posteromedian area impunctate, surface somewhat dulled by delicate reticular shagreening, especially anteriorly and laterally; scutellum with crowded punctures and delicate shagreening; mesepisternum with lateral surface punctures slightly smaller than largest mesoscutal punctures, surface shiny, slightly or not at all shagreened; metasomal tergum 1 with basal three-fifths punctate but punctures crowded only in basal fourth, elsewhere punctures separated mostly by two to four puncture widths, apical area impunctate, surface dulled by reticulotransverse shagreening; tergum 2 with basal zone with punctures separated by half a puncture width and surface dulled by reticular shagreening, interband zone with scattered punctures of irregular size, apical area impunctate, surface moderately shiny, with reticulotransverse shagreening; tergum 3 similar to tergum 2 but interband zone with distinct, round, regular punctures separated mostly by less than one puncture width; pygidial plate U-shaped with sides diverging towards base, sides subparallel in apical third (when not worn).

Hair: Head white to pale ochraceous except dark brown on vertex. Thorax pale ochraceous on lower lateral surfaces, ochraceous to yellow elsewhere except scutellum dark brown medially and mesoscutum with posteromedian dark brown patch which extends forward to a transverse line usually at about middle of tegulae. Metasomal tergum 1 ochraceous basally, glabrous apically; tergum 2 with pale ochraceous to white pubescence in basal zone connected by pale pubescence to short, pale, strongly oblique, lateral, pubes-

cent fasciae which quite or almost reach apical margin of tergum at extreme sides, apical area glabrous, interband zone with scattered, minute, pale brown, simple, suberect to appressed hairs, tergum 3 similar to tergum 2 but basal tomentum brown, apical area narrow (equals half of distal pale band medially), distal pale band uninterrupted medially and interband zone with diffuse, pale, appressed pubescence; tergum 4 similar to tergum 3 but distal pale band apical and never interrupted medially; terga 5 and 6 medially usually golden to pale brown and white at extreme sides; sterna with golden hairs medially to white laterally. Legs with hairs white except as follows: inner surfaces of tarsi yellow to orange; outer surface of fore basitarsi brown.

Male. Measurements and ratios: N, 17; length, 9-12 mm.; width, 2.5-3.5 mm.; wing length, $M = 3.27 \pm 0.116$ mm.; hooks in hamulus, $M = 11.31 \pm 0.198$; flagellar segment 2/segment 1, $M = 5.05 \pm 0.143$.

Structure and color: Integumental color as in *M. lupina* but apical areas of terga usually somewhat translucent, yellowish brown to brown. Structure as in *lupina* except as follows: flagellar segments 4 to 10 with longitudinal dorsolateral shiny depressions, minimum length of first flagellar segment equals more than one-fifth of maximum length of second segment, ultimate segment about three times as long as broad, penultimate segment more than twice and less than three times as long as broad; maxillary palpal ratio about 4:3:3:1 or last segment shorter; galeae moderately shiny above, dulled by delicate shagreening at least in apical half; apical margin of fourth sternum extremely broadly and shallowly emarginate or evenly convex. Sculpturing as in female except as follows: mesoscutum with posteromedian area often with scattered punctures; metasomal tergum 1 with basal four-fifths to five-sixths with coarse punctures irregularly spaced by less than one to three puncture widths; tergum 2 with interband zone with large round punctures separated mostly by one or less puncture widths, punctures as large as on base of tergum 1; tergum 3 similar to tergum 2 but punctures of interband zone more crowded; terga 4 and 5 similar to tergum 3.

Sternum 7 similar to that of *M. plumosa* with the following additions: median plate with apical margin transverse or almost so, with lateral concavity at side of neck about as long as median plate above the concavity; lateral plate with apicomedian edge expanded slightly so that it slightly surpasses apicolateral process; membranous area large, subtriangular (Fig. 58). Sternum 8 as in

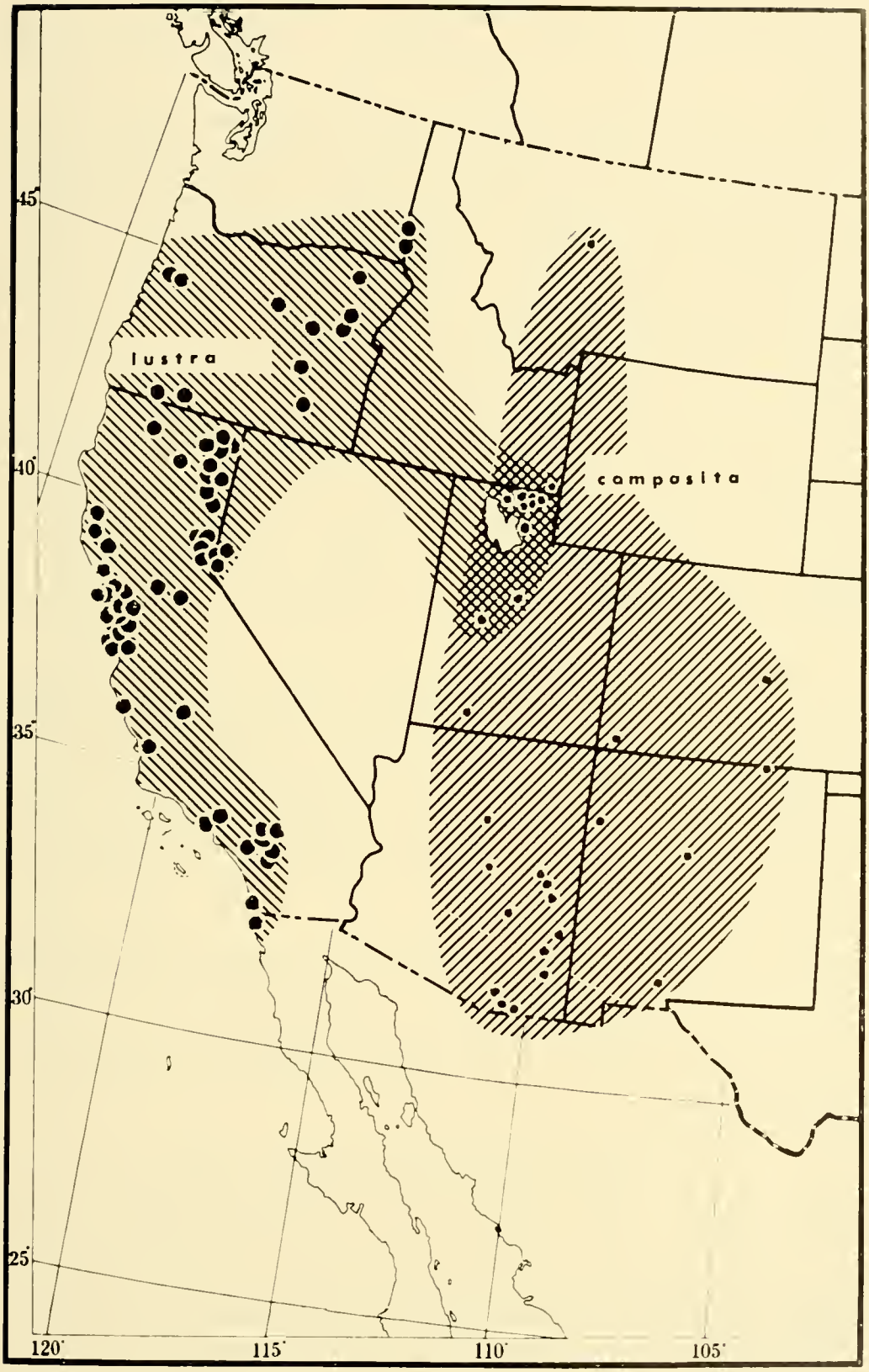

FIG. 7. Map showing the known distributions of *M. (Callimelissodes) lustra* LaBerge and *M. (C.) composita* Tucker.

plumosa but with several short, delicate hairs on apical margin at either side of median emargination. Genital capsule as in *plumosa.*

Hair: Head and thorax pale to dark ochraceous, usually darker on vertex of head and on dorsum of thorax. Metasomal terga white to ochraceous with the following additions: terga 2 to 4 with apical areas glabrous; tergum 5 with distal pubescent band usually reaching margin; terga 6 and 7 dark ochraceous to pale brown (brown especially basally and medially). Legs with pale ochraceous to white hairs except inner surfaces of tarsi yellow to pale orange.

Type Material. Holotype male and two male paratypes collected by E. S. Tucker at Colorado Springs, Colorado, at 5915 feet altitude, August, 1906. The holotype is in the U. S. National Museum (Type No. 12878) and the two paratypes are in the Snow Entomological Collection of the University of Kansas, Lawrence, Kansas. In addition to the type material, 57 females and 15 males from the localities listed below have been examined (Fig. 7). This list includes localities reported in the literature.

ARIZONA: Canelo; Flagstaff (3 miles N. W. and 7 miles S.); Globe; Granville (20 miles N.); Huachuca Mts.; Lakeside; McNary Junction, Apache Reservation (6 miles S.), Apache Co.; Pine; Safford (30 miles S.); Santa Rita Mts. COLORADO: Berkeley; Colorado Springs; Mesa Verde. IDAHO: Cub River Canyon; Franklin. MONTANA: Cascade Co. NEW MEXICO: Gallup; Las Cruces; Raton Pass; Sandia Mts. UTAH: Glendale; Green Canyon; Howell; Logan Canyon; Mendon; Mt. Nebo.

Flower Records. Not much data is available concerning the flower preferences of this species. This data, however, indicates a preference for plants of the family Compositae.

Aster sp., *Grindelia* sp., *G. squarrosa, Haplopappus gracilis, Thurberia thespesioides.*

Melissodes (Callimelissodes) lustra, n. sp.

This species is closely allied to *M. composita* Tucker. The females are distinguished from those of *composita* primarily by the less coarse punctation of the mesoscutum and first metasomal tergum. The males of *lustra* can be distinguished from those of *composita* by the less coarse sculpturing of the mesoscutum and by the shape of the median and lateral plates of sternum 7 as described below.

Female. Measurements and ratios: N, 20; length, 9-12 mm.; width, 3.0-4.5 mm.; wing length, $M = 3.56 \pm 0.168$ mm.; hooks in

hamulus, M = 12.70 ± 0.147; flagellar segment 1/segment 2, M = 2.05 ± 0.027.

Structure and color: Integumental color as in *lupina* except eyes yellowish green to green. Sculpturing and structure as in *composita* with the following differences: supraclypeal area often dulled by reticular shagreening; maxillary palpal segments in ratio of about 2:2:2:1; mesoscutum with punctures mesad of parapsidal lines small to minute, separated mostly by more than one puncture width (often by three or four puncture widths), punctures laterad of parapsidal line small, separated by one-half to one puncture width, posteromedian impunctate area large; scutellar punctures irregular in size, medially separated by one-half to two puncture widths; mesepisterna with punctures shallow, as large or larger than mesoscutal punctures mesad of parapsidal lines, surface dulled by fine shagreening; metasomal tergum 1 with basal sixth with crowded punctures, from basal sixth to about three-fifths of median length with scattered punctures separated by two to four puncture widths, apical area impunctate; tergum 2 with basal zone punctures minute, separated mostly by one puncture width and surface shiny, interband zone with scattered, irregular-sized punctures, apical area impunctate, surface moderately shiny, reticulotransversely shagreened; tergum 3 similar to tergum 2 but interband zone punctures sparser than in *composita*, medially separated mostly by two or more puncture widths; pygidial plate narrow, U-shaped with sides subparallel in apical third (somewhat V-shaped when worn near tip).

Hair: Hair color as in *composita* with the following additions: head often with dark brown mixed with pale on face along inner margins of compound eyes (as in holotype) to occasional specimens in which head all dark brown except golden on labrum; thorax often with a few long brown hairs mixed with the pale on pronotum (as in holotype) and especially on posterior pronotal lobes to occasional specimens in which lateral surfaces of thorax and pronotum with all hairs dark brown to black and dark mixed with the pale on anterior and lateral parts of mesoscutum; metasomal terga 5 and 6 occasionally with median hairs dark brown (golden in holotype and in most specimens, even on some in which the head and thorax are mostly dark); legs with hairs as in *composita* (and in holotype of *lustra*) but darkest specimens with coxae, trochanters, femora and fore tibiae pale brown and inner surfaces of hind basitarsi red.

Male. Measurements and ratios: N, 20; length, 9-12 mm.; width, 2.5-3.5 mm.; wing length, M = 3.31 ±0.153 mm.; hooks in hamu-

lus, M = 11.95 ± 0.185; flagellar segment 2/segment 1, M = 3.45 ± 0.067.

Structure and color: Integumental color as in *composita* but eyes yellowish green. Structure and sculpturing as in *composita* with the following differences: minimum length of first flagellar segment equals one-third to one-fourth maximum length of second segment (one-third in allotype); maxillary palpal segments in ratio of about 3.0:3.0:2.5:1.0; mesoscutum with punctures smaller and sparser, mesad of parapsidal lines separated by one to two puncture widths; mesepisternum with surface dulled by reticular shagreening; metasomal tergum 1 with basal four-fifths or less punctate; tergum 2 with basal zone punctures separated mostly by one or more puncture widths; interband zone punctures small, irregular, separated by one-half to three puncture widths; tergum 3 with interband zone punctures small, separated mostly by one to two puncture widths; tergum 4 as in tergum 3; terga 2 to 5 with apical areas shiny, with extremely delicate reticulotransverse shagreening.

Sternum 7 as in *composita* except as follows: median plate with apical margin oblique, slanting proximad towards outer side, with lateral concavity at side of neck small, deep, about half as long as plate above the concavity; lateral plate with apicomedian margin not expanded distad, but mesal margin in a rounded, continuous slope from apicolateral process mesally and proximally to membranous area (Fig. 59). Sternum 8 and genital capsule as in *composita.*

Hair: Vestiture of head and thorax cinereous to ochraceous and often brighter (even slightly rufescent) on vertex and dorsum of thorax. Abdominal and leg hairs and pubescence as in *composita.*

Remarks. Although a number of Californian specimens (all females) tend to be dark in vestiture color, these specimens are not so distributed geographically nor abundant enough to warrant recognition as a separate subspecies. The darkest females come from Millbrae in San Mateo County and Gazelle in Sonoma County and are only four in number. Other specimens with dark hairs scattered especially over the face and pronotum occur in several localities in California (including the type locality) and in Oregon.

M. lustra is extremely similar to *M. composita.* Also, the two species are largely allopatric in distribution, their ranges overlapping only in Utah and southern Idaho. These facts may suggest that *lustra* is nothing but a well-marked subspecies of *composita.* However, the fact that there are localities in Utah and in Idaho

in which both species have been collected at the same time without any obvious intergrades seems to provide convincing evidence that the two forms are distinct species.

M. lustra is an oligolectic bee depending upon plants of the family Compositae for pollen and, particularly, upon the genera *Gutierrezia, Chrysothamnus* and *Isocoma* in decreasing order of importance. Of 63 collections of bees in which the floral data is recorded, 61 are from one of 14 genera of composites. The other two collections consist each of a single male from a legume (*Melilotus alba*) and a euphorb (*Croton californicus*). Of the 44 collections of bees from composites, 17 were taken from flowers of species of *Gutierrezia.*

Type Material. The holotype female, allotype male and eleven female and one male paratypes were collected by C. D. Michener at Erwin Lake, San Bernardino Mts., California, on August 22, 1932. An additional male paratype was taken in the same locality by C. D. Michener on August 18, 1932. Additional paratypes from California include 33 females and 5 males as follows: Baldwin Lake, San Bernardino Co.: 3 females on *Chrysothamnus viridulus,* September 1, 1936, P. H. Timberlake. Big Bear Lake, San Bernardino Co.: 1 male, August 7, 1930, L. Wilson. Riverside, Riverside Co.: the following collected by P. H. Timberlake on *Gutierrezia sarothrae:* 1 female on October 17, 1924, 1 female on October 20, 1924, 1 female on October 9, 1925, 1 female on October 13, 1925, 3 females on October 22, 1925, 1 female on October 26, 1925, 1 female on October 27, 1925, 3 females on October 28, 1925, 3 females on November 4, 1925, 1 female on November 10, 1925, 1 female on November 16, 1925, 1 female on November 19, 1925, 1 female on October 24, 1927, 1 female on October 15, 1929, 1 female on October 16, 1929, 1 female on November 5, 1929; the following collected by P. H. Timberlake on *Gutierrezia californica:* 1 female on September 22, 1926; the following collected by P. H. Timberlake on *Ericameria palmeri:* 1 male on September 25, 1925, 1 female on November 6, 1928, 1 female on October 9, 1929, 2 males on October 28, 1929; the following collected by P. H. Timberlake on *Isocoma vernonioides:* 1 female on October 10, 1926, 1 female on October 31, 1932, 1 female on October 3, 1934; 1 female on October 20, 1951, P. D. Hurd. Whitewater, Riverside Co.: 1 male, October 27, 1934, A. L. Melander. Whitewater Canyon, Riverside Co.: 1 female on *Isocoma* sp., October 14, 1951, P. H. Timberlake. The holotype and allotype are in the Snow Entomological Museum of the Uni-

versity of Kansas, Lawrence. Paratypes are in the Snow Entomological Museum and in the collections of P. H. Timberlake, Citrus Experiment Station, Riverside, California, the University of California at Berkeley, the University of California at Davis, the Museum of Comparative Anatomy at Harvard University, Cambridge, Massachusetts, and in the author's personal collection.

Distribution. M. lustra occurs from Baja California in the southwest, north to Oregon and east to Utah and Idaho (Fig. 7). It has been collected between the dates of August 7 and November 19 (one label bears the month of July and the specimen was presumably taken near the end of that month). A total of 235 females and 182 males have been examined from the localities listed below (including type material).

CALIFORNIA: Alturas; Antioch; Avon; Baldwin Lake; Benecia; Berkeley; Big Bear Lake; Boca Dam (11 miles E. of Truckee); Brookway; Caliente Mt., San Luis Obispo Co.; Calpine; Canby; Capitola; Carbon; Cedar Pass, Modoc Co.; Deep Creek; Erwin Lake, San Bernardino Mts.; Gazelle; Halleleujah Junction, Lassen Co.; Hobart Mills; Kentfield; Lake City; Larkspur; Lemoore; Livermore; Los Angeles Co.; Lucia; Madeline (and 8 miles N.); Mason Creek Railroad Siding, Modoc Co.; McArthur; Mt. Tamaulpais; Murphys; Menlo Park; Millbrae; Palo Alto; Ravendale (8 miles S.); Riverside; Sacramento; San Diego; San Francisco Bay; San Jose; Sonoma Co.; Santa Clara Co.; Sierraville (and 8 miles N. W.); Soda Bay, Clear Lake; Standish (4 miles W.); Stanford University; Tesla; Truckee (2 miles N.); Ukiah; Vallejo; West Hollywood Hills; Westwood Hills; Whitewater; Whitewater Canyon. IDAHO: Cub River Canyon; Franklin; Lewiston; Moscow. NEVADA: Purdy; Reno (2 miles N.); Sparks (11 miles N.); Washoe City. OREGON: Antelope Mt., Harney Co.; Baker; Burns (23 miles E.); Corvallis; Elgin (3 miles S.); Hereford; Klamath Lake; Medford; Mitchell (14 miles E.); Prairie City; Tangent (5 miles E.). UTAH: Cache Junction; Delta; Honsel; Logan Canyon; Mendon; Ogden. *Mexico.* BAJA CALIFORNIA: Tijuana (32 miles S.).

Flower Records. Aster sp., *Baccharis pilularis, Biglovia* sp., *Chrysothamnus* sp., *C. nauseosus, C. nauseosus consimilis, C. nauseosus speciosus, C. v. viscidiflorus, C. viridulus, Croton californicus, Ericameria palmeri, Eriogonum latifolium, Grindelia* sp., *G. camporum, Gutierrezia californica, G. sarothrae, Haplopappus bloomeri angustatus, Helianthus* sp., *Heterotheca grandiflora, Isocoma* sp., *I. vernonioides, Melilotus alba, Senecio douglasii.*

Melissodes (Callimelissodes) glenwoodensis Cockerell

Melissodes glenwoodensis Cockerell, 1905, Ann. Mag. Nat. Hist., ser. 7, vol. 15, p. 522; 1905, Canadian Ent., vol. 37, p. 321; 1906, Trans. Amer. Ent. Soc., vol. 32, pp. 107, 113; 1906, Trans. Amer. Ent. Soc., vol. 32, p. 309; 1927, Ann. Ent. Soc. Amer., vol. 20, p. 396.

This strikingly marked bee is closely related to *Melissodes lustra* from which it differs in both sexes primarily by its larger size. The females of *glenwoodensis* can be distinguished further by the dark reddish brown hairs on the inner surfaces of the hind basitarsi and tibiae. The males are distinguished from those of *lustra* by the lack of the longitudinal, dorsolateral depression on flagellar segment four and by usually having dark brown hairs on terga 6 and 7.

Female. Measurements and ratios: N, 20; length, 11-14 mm.; width, 4-5 mm.; wing length, $M = 4.23 \pm 0.171$ mm.; hooks in hamulus, $M = 14.15 \pm 0.233$; flagellar segment 1/segment 2, $M = 2.04 \pm 0.022$.

Structure and color: Integument black except distitarsi, apical half of mandible and lower surface of flagellar segments 3 to 10 rufescent, eyes gray to greenish gray and basitibial spurs red to yellow. Sculpturing and structure as in *composita* except as follows: clypeus with surface dulled by fine shagreening; supraclypeal area dulled by dense reticular shagreening; flattened area of vertex posteromesad of apex of compound eye with small punctures separated by one to two puncture widths, surface dulled by fine shagreening; galeae above dulled by reticular shagreening at least in apical half; maxillary palpal ratio about 2.0:2.0:1.5:1.0, with last segment sometimes slightly shorter; mesoscutum with large round punctures anteriorly and laterally, punctures just mesad and just laterad of parapsidal lines separated by one puncture width or less, surface with fine tessellation at least anteriorly, posteromedian area impunctate or with scattered punctures separated mostly by two or more puncture widths; scutellar punctures small, separated by one-half to two puncture widths; mesepisternal punctures shallow, round, separated by half a puncture width or less, surface dulled by tessellation; metasomal tergum 1 with crowded punctures in basal third or less, with scattered, minute punctures in middle third, apical area impunctate, surface reticulotransversely shagreened, shiny apically; tergum 2 with basal zone punctures minute, round, crowded, with interband zone punctures mostly minute, extremely sparse, with apical area impunctate, surface shiny, reticulotransverse shagreening extremely fine; tergum 3 similar to tergum 2 but interband zone punctures minute, round, separated by one to two

puncture widths, surface shiny (especially apical area); pygidial plate V-shaped with rounded apex.

Hair: Palest specimens with head white except a few brown hairs on vertex; darkest with abundant dark brown hairs on vertex and surrounding hairs ochraceous. Thorax of palest white below to pale ochraceous above; darkest pale ochraceous below to ochraceous above and mesepisternum with anterior surface dark ochraceous to brown. Metasomal tergum 1 with basal area and at extreme sides with white to pale ochraceous hairs; tergum 2 with basal pubescense white, with distal pubescent band restricted to narrow, lateral, oblique, white fasciae each equaling slightly more than apubescent median area in width and laterally separated from apical margin by at least length of fascia at that point; tergum 3 with basal tomentum dark brown, distal pubescent band white, separated from apical margin across entire tergum, interband zone with scattered pubescence brown to white (brown nearer base); tergum 4 with apical pubescent band white, uninterrupted medially, basal and interband zones as in tergum 3; terga 5 and 6 dark brown to black except lateral tufts of long white or ochraceous hairs (sometimes absent on tergum 6); sternal hairs dark brown, with or without white laterally. Legs of palest specimens pale ochraceous except as follows: scopal hairs pale yellow; basitibial plates pale brown; inner surfaces of basitarsi and fore and hind tibiae dark brown to dark reddish brown; coxae, trochanters and at least proximal part of inner surfaces of femora brown. Darkest with legs similar but with more abundant brown hairs on femora, trochanters and coxae and scopal hairs bright yellow except brown at apex of basitarsi.

Male. Measurements and ratios: N, 20; length, 10-15 mm.; width, 3.5-4.5 mm.; wing length, $M = 3.98 \pm 0.277$ mm.; hooks in hamulus, $M = 13.25 \pm 0.176$; flagellar segment 2/segment 1, $M = 3.78 \pm 0.085$.

Structure and color: Integumental color as in *lupina* except eyes usually green to grayish green. Structure as in *composita* except as follows: flagellar segments 5 to 10 with longitudinal, dorsolateral depressions (segment 4 occasionally with depression weakly developed near apex); minimum length of first flagellar segment equals about one-fourth maximum length of second segment; maxillary palpal segments in ratio of about 4:4:3:1, last segment often slightly longer; galeae shiny to moderately so above, dulled by reticular shagreening at least in apical half; sternum 4 with apical margin convex, sterna 3 and 5 with apical margins ex-

tremely weakly convex, almost straight. Sculpturing as in female except as follows: mesoscutum more densely punctate, posteromedian area with punctures separated mostly by one to two puncture widths; metasomal tergum 1 with basal two-thirds to three-fourths punctate, punctures separated by one-half (at extreme base) to one puncture width or more; tergum 2 with interband zone with more crowded punctures of irregular size separated mostly by one to two puncture widths; terga 3 and 4 similar to tergum 2 in interband zone but punctures more crowded and smaller; terga 2 to 5 with surfaces of interband zones dulled by distinct reticular shagreening, apical areas highly shiny as in female.

Terminalia essentially as in *lustra* except as follows: sternum 7 with lateral plate with apicomedian margin slightly expanded but not so as to exceed apicolateral process as in *composita;* spatha usually with apicomedian emargination slightly shallower than in either *composita* or *lustra* (Figs. 60-63).

Hair: Vestiture essentially as in *composita* except as follows: generally hair and pubescence more white than in *composita;* pubescent bands of metasomal terga usually white; terga 6 and 7 with hairs dark brown or at least largely so; sternal hairs often brown medially; tergum 5 with distal pubescent band separated from apical margin at least medially.

Remarks. Specimens from southern California are generally paler in color and smaller in size than from elsewhere in the range of this species. These differences are not distinct enough nor constant enough to permit the recognition of a separate subspecies. The darkest specimens are most abundant in Colorado and Utah, but appear sporadically from Oregon and California as well.

This species is apparently restricted to plants of the family Compositae for pollen sources. All of the 146 bees bearing floral data (representing 29 collections) were collected from composites (seven genera). Of these 29 collections 20 were made on flowers of *Chrysothamnus* which seems to be of special importance as a pollen source in several parts of the range of the species.

Type Material. The holotype female of *glenwoodensis* collected by Gillette at Glenwood Springs, Colorado, August 15, 1903, is in the collection of P. H. Timberlake of the Citrus Experiment Station at Riverside, California.

Distribution. M. glenwoodensis ranges from southern California north to Washington, east to North Dakota and southeast to Colorado, New Mexico and Utah (Fig. 8). It has been collected from

June 29 to November 4 but mainly during August and September. A total of 73 females and 232 males have been examined, including the holotype, from the localities listed below.

CALIFORNIA: Benton; Big Pine, Inyo Co.; Bridgeport, Mono Co.; Gazelle, Siskiyou Co.; Hallelujah Junction (10 miles N.), Lassen

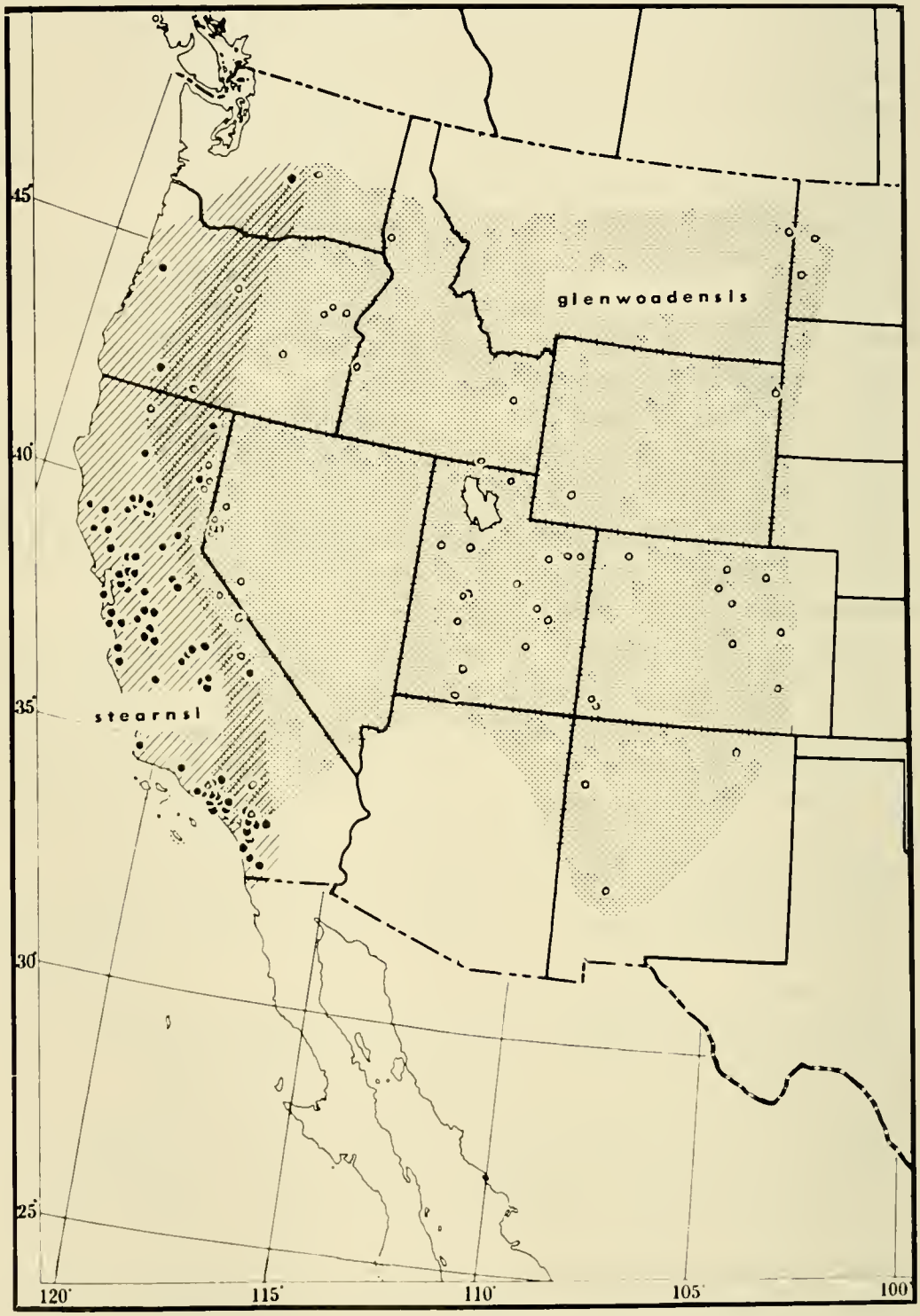

FIG. 8. Map showing the known distributions of *M. (Callimelissodes) stearnsi* Cockerell and *M. (C.) glenwoodensis* Cockerell.

Co.; Helendale; Litchfield; Oro Grande, San Bernardino Co.; Pasadena Quadrangle (Bailey Canyon), San Gabriel Mts.; Ravendale (15 miles S.); Riverside; Sierra Nevadas; Standish (4 miles W.). Colorado: Colorado Springs; Cortez; Denver; La Junta; Limon; Masonville, Mesa Verde; Moffatt Co.; Platte Canyon; White Rocks (Boulder). Idaho: Coyote Grade, Nez Perce Co.; Homedale; Idaho Falls; Stone. Montana: Fairview. Nevada: Reno (and 2 miles N. and 14 miles N. E.); Sparks (17 miles N.); Sutcliffe; Walker Lake. New Mexico: Maxwell; McGaffey; Winston. North Dakota: Medora (10 miles W.); Schafer. Oregon: Baker (10 miles S.); Burns (23 miles E.); Durkee, Baker Co.; Grizzly Butte; Hereford; Klamath Falls (15 miles E.). Utah: Allen Canyon; Amalga; Bryce Canyon; Cache Junction; Clear Creek Canyon; Cove Fort; Delta; Deseret; Dugway Parade Ground, Tooele Co.; Emery Co.; Green River; Hanksville; Johnsons Pass, Tooele Co.; Kaibab Forest; Logan Canyon; Roosevelt; Skull Valley (Orr's Ranch); Tridell; Vernal. Washington: Soap Lake, Grant Co. Wyoming: Clifton, Weston Co.; Granger.

Flower Records. *Aster* sp., *Chrysothamnus* sp., *C. nauseosus consimilis, C. v. viscidiflorus, Cirsium* sp., *Grindelia* sp., *G. squarrosa, Helianthus* sp., *H. petiolaris, Isocoma vernonioides, Solidago* sp., *S. trinervata.*

Melissodes (Callimelissodes) tuckeri Cockerell

Melissodes tuckeri Cockerell, 1909, Canadian Ent., vol. 41, p. 129.

This species is readily recognized in both sexes by its extremely coarse punctation on all parts of the body. Areas which are normally impunctate or finely punctate in *Melissodes*, such as the genal areas lateral to the eyes, in *M. tuckeri* have crowded, deep, coarse punctures. *M. tuckeri* is not closely related to any of the foregoing species, but judging from the male antennae, the male terminalia and the punctation, it is probably closest to *M. composita.*

Female. Measurements and ratios: N, 12; length, 10-12 mm.; width, 3.5-4.0 mm.; wing length, M = 3.72 ± 0.215 mm.; hooks in hamulus, M = 13.83 ± 0.322; flagellar segment 1/segment 2, M = 1.80 ± 0.025.

Structure and color: Integument as in *M. lupina* except eyes green and wing membranes somewhat infumate, yellow to yellowish brown. Clypeus with large punctures separated by less than half a puncture width, surface shiny, unshagreened or slightly so; supraclypeal area with a few large punctures or impunctate me-

dially, surface shiny to somewhat dulled by delicate shagreening; vertex with flattened areas posteromesad of compound eyes with small, crowded, deep punctures separated by less than one puncture width, surface dulled by fine reticular shagreening; genal areas lateral to compound eyes with deep round punctures separated mostly by half a puncture width; face coarsely punctate everywhere except narrow zone just mesad of upper half of compound eye and these zones usually dulled by fine tessellation; ultimate flagellar segment longer than broad; galeae moderately shiny above, dulled by fine reticular shagreening at least in apical half; maxillary palpal segments in ratio of about 3.5:3.5:3.0:1.0. Mesoscutal punctures extremely coarse, separated everywhere by half a puncture width or less, near parapsidal lines separated by one-fourth of a puncture width, surface unshagreened; scutellar punctures similar to mesoscutal but slightly smaller; mesepisternum with punctures of lateral surface extremely large, shallow, almost confluent with only a narrow ridge separating one from another, bottoms of punctures usually finely tessellate; metanotum with punctures almost as large as scutellar; propodeum with dorsal surface reticulopunctate, posterior surface with impunctate upper triangular area and coarsely punctate elsewhere, lateral surfaces coarsely punctate, surfaces dulled by coarse tessellation. Metasomal tergum 1 with basal half or slightly less with small round deep punctures separated by one-half to one puncture width, apical to this punctures become progressively smaller and sparser and apical one-fourth or less impunctate, surface shiny, with extremely fine reticulotransverse shagreening; tergum 2 with interband and basal zones punctate as at base of tergum 1 but punctures slightly smaller, with apical area with conspicuous punctures which are smaller and sparser medially and become smaller and sparser apically, with narrow apical impunctate margin; tergum 3 similar to tergum 2 but apical punctate area restricted to median third and punctures slightly more crowded; tergum 4 as in tergum 3 but without apical area and punctures smaller and more crowded; pygidial plate broadly V-shaped with rounded apex.

Hair: Vestiture as in *composita* with the following differences: pale hairs, especially of vertex and dorsum of thorax, usually darker ochraceous; vertex with more abundant dark brown hairs; mesoscutal dark patch extends forwards to a transverse line at anterior margins of tegulae; tegulae brown; terga 1 to 3 with apical areas with short, suberect to appressed dark brown hairs; tergum 2 with in-

terband zone with suberect to appressed dark brown hairs and white distal and basal bands not or only narrowly connected at sides, with distal pale band interrupted medially by at least width of lateral fascia; tergum 3 with distal band interrupted medially or with rounded posterior median notch which almost interrupts pale band, without white pubescence in interband zone; terga 5 and 6 dark brown to black except long pale lateral tufts; sternal hairs brown to reddish brown medially; legs with dark brown to dark reddish brown hairs on fore tarsi, on fore and middle tibiae near apices of outer surfaces, on inner surfaces of basitarsi and surrounding basitibial plates.

Male. Measurements and ratios: N, 8; length, 9-11 mm.; width, 2.5-3.5 mm.; wing length, M = 3.37 ± 0.375 mm.; hooks in hamulus, M = 11.75 ± 0.250; flagellar segment 2/segment 1, M = 4.44 ± 0.173.

Structure and color: Integumental color as in *lupina* but eyes yellowish gray to grayish green and wing membranes somewhat infumate, yellow. Structure as in *plumosa* except as follows: minimum length of first flagellar segment equals about one-fourth of maximum length of second segment; penultimate flagellar segment about twice as long as broad; flagellar segments 3 to 10 with longitudinal, ventrolateral, shiny depressions; maxillary palpal segments in ratio of about 12:9:9:1, last segment often twice as long. Sculpturing as in female except as follows: metasomal tergum 1 with basal four-fifths to five-sixths coarsely punctate with punctures large as scutellar punctures and separated by half a puncture width or less; tergum 2 with punctures of interband and basal zones large, deep, separated by half a puncture width or less, with apical area with distinct punctures in basal half or less; terga 3 and 4 similar to tergum 2 but punctures slightly smaller and more crowded.

Terminalia essentially as in *plumosa* except as follows: sternum 7 with lateral plate with apicomedian margin expanded apically much as in *composita,* with median plate much broader than in *plumosa;* sternum 8 with a few short hairs apically at each side of median emargination; gonostylus with short hairs on outer surface near base and along inner margin.

Hair: Vestiture as in *plumosa* except as follows: vertex often with a few brown hairs; mesoscutum with brown hairs posteromedially; metasomal terga 6 and 7 with abundant dark brown hairs; sternal hairs often yellowish brown to yellow medially.

Type Material. Holotype female from Plano, Texas, October 1907, E. S. Tucker, is in the collection of P. H. Timberlake at the Citrus Experiment Station, Riverside, California.

Distribution. This species is distributed from Montana south to Texas in the prairies (Fig. 6). It is seemingly a rare species and has been collected infrequently during the months of September and October. A total of 13 females and 8 males, including the holotype, have been examined. The collection data for these is given in full, since so few specimens are involved.

KANSAS: Douglas Co., 1 male on *Aster* sp., October 15, 1949, C. D. Michener; Lawrence, 1 female, September 29, 1954, C. Fitch. MONTANA: Glendive, 1 female, C. N. Ainslie. NEBRASKA: Lincoln, 2 males during September. SOUTH DAKOTA: Cedar Pass (Badlands), 3 males, August 14, 1940, H. E. Milliron; Midland, 1 male, September 10, 1935, A. G. Peterson; Slim Buttes, 2 females, September 7, 1940, H. C. Severin. TEXAS: Brazos Co., 5 females and 1 male on *Aster* sp., October 10, 1954, A. H. Alex, 1 female on *Heterotheca subaxillaris*, October 17, 1955, A. H. Alex; Plano, 2 females, October 1907, E. S. Tucker.

Melissodes (Callimelissodes) coloradensis Cresson

Melissodes coloradensis Cresson, 1878, Proc. Acad. Nat. Hist. Philadelphia, vol. 30, p. 200; Robertson, 1894, Trans. Acad. Sci. St. Louis, vol. 6, pp. 454-476; 1896, Trans. Acad. Sci. St. Louis, vol. 7, pp. 176-178; 1898, Botanical Gazette, vol. 25, p. 244; 1905, Trans. Amer. Ent. Soc., vol. 21, p. 368; Cockerell, 1906, Trans. Amer. Ent. Soc., vol. 32, pp. 78, 80, 83, 88; Robertson, 1914, Ent. News, vol. 25, p. 70; Cresson, 1916, Mem. Amer. Ent. Soc., vol. 1, p. 115; Robertson, 1926, Ecology, vol. 7, p. 380; 1928, Flowers and Insects, p. 8; Pearson, 1933, Ecol. Monogr., vol. 3, pp. 381, 392, 493; Graenicher, 1935, Ann. Ent. Soc. Amer., vol. 28, p. 304; Brimley, 1938, Insects of North Carolina, p. 462; Bohart, Knowlton and Bailey, 1950, Utah State Agric. Coll. Mimeo. Series No. 371, p. 5.

This large, distinctively colored bee is readily distinguished from the other members of the subgenus *Callimelissodes*. It superficially resembles *Svastra obliqua* (Say), but can be separated from that species by the shape of the tegulae which are narrowed anteriorly as in all species of the genus *Melissodes*. *M. coloradensis* can be separated from other species of the subgenus *Callimelissodes* in both sexes by the deeply infumate wings, the yellow-ochre color of the pale vestiture, the coarsely punctate integument (although less coarse than in *M. tuckeri*) and its large size (equaled only by some specimens of *M. glenwoodensis* in this subgenus). It is most closely related to *M. tuckeri* than to any other members of the subgenus.

Female. Measurements and ratios: N, 20; length, 13-16 mm.;

width, 4.5-6.0 mm.; wing length, M = 5.25 ± 0.126 mm.; hooks in hamulus, M = 16.20 ± 0.304; flagellar segment 1/segment 2, M = 1.99 ± 0.022.

Structure and color: Integument black except as follows: distitarsi, apical half of mandible and lower surface of flagellar segments 3 (often apex of 2) to 10 rufescent; wing membranes deeply infumate, brown; eyes dark gray to greenish gray.

Clypeus with small round punctures separated mostly by half a puncture width or less, surface dulled by coarse reticular shagreening; supraclypeal area similar to clypeus but punctures larger medially; vertex with flattened area posteromesad of compound eye with small round punctures separated by half to one puncture width, surface dulled by fine shagreening; eye about 3 times as long as broad; galeae dulled above by fine tessellation; maxillary palpal segments in ratio of about 2.5:3.0:2.0:1.0, last segment variable. Mesoscutum with deep round punctures separated by less than one-half to somewhat more than one puncture width, slightly more crowded anteriorly and laterally than posteromedially, surface shiny, with extremely delicate shagreening or unshagreened; scutellar punctures similar to mesoscutal but average slightly smaller; metanotal punctures half diameter of large scutellar punctures, crowded, mediodorsally separated by about half a puncture width, surface minutely tessellate; propodeum as in *M. lupina* but dorsal surface in apical half with punctures elongate and orientated anterolaterally; mesepisternum with punctures similar in size and spacing to anterior mesoscutal punctures, surface shiny. Metasomal tergum 1 with basal four-fifths punctate, punctures about same diameter as scutellar, smaller towards apical margin, separated by one-half to two puncture widths but mostly by less than one, apical area impunctate, surface dulled by extremely fine, dense, reticulotransverse shagreening; tergum 2 with abundant deep punctures of same size as in tergum 1 or slightly smaller, in basal zone separated by half a puncture width or less, in interband zone separated mostly by one-half to one puncture width, in apical area crowded basally and becoming smaller and sparser apically until apical one-third of apical area impunctate, surface shagreened as in tergum 1; terga 3 and 4 similar to tergum 2 but punctures slightly smaller and more crowded; pygidial plate U-shaped with arms diverging widely towards base.

Hair: Head ochraceous below to yellow-ochre above and vertex with abundant dark brown hairs. Thorax yellow-ochre laterally

to slightly rufescent on anterior part of mesoscutum and pronotum; mesoscutal posteromedian dark brown patch extending laterally to tegulae or almost so and anteriorly to a transverse line at anterior margins of tegulae; tegulae dark brown; scutellum dark brown, narrowly fringed with ochraceous. Metasomal tergum 1 with long yellow-ochre hairs in basal third, apically with minute, simple, appressed, dark brown hairs; tergum 2 with pale ochraceous pubescence at extreme base, with narrow, short, lateral fasciae of ochraceous pubescence distally which equal less than one-third of tergum and in length about half of apubescent area apical to them, not connected with basal pubescence at extreme sides, interband and apical zones with short, closely appressed, simple, dark brown hairs; tergum 3 similar to tergum 2 except basal tomentum dark brown, lateral pale fasciae broader than one-third of width of tergum (occasionally with distal pale band only narrowly interrupted medially) and as long as or longer than apical apubescent area; tergum 4 similar to tergum 3 but distal pale band reaches apical margin except in median one-fourth to one-third, uninterrupted medially; terga 5 and 6 dark brown except pale ochraceous tufts at sides; sternal hairs reddish brown medially to ochraceous laterally. Legs brown except as follows: coxae, trochanters and femora (except at tips) yellow-ochre to ochraceous; inner surfaces of tarsi (including hind basitarsi) red to reddish brown; scopal hairs yellow except brown near apex of basitarsus and near basitibial plate.

Male. Measurements and ratios: N, 20; length, 13-16 mm.; width, 4.0-5.5 mm.; wing length, $M = 4.88 \pm 0.240$ mm.; hooks in hamulus, $M = 15.05 \pm 0.198$; flagellar segment 2/segment 1, $M = 6.40 \pm 0.103$.

Structure and color: Integumental color as in female with the following differences: clypeus and base of mandible bright yellow; labrum white; flagellar segments 3 to 11 yellow to red below; wing membranes infumate, yellowish brown, veins dark reddish brown; eyes gray to green.

Structure as in *lupina* except as follows: eyes about two and one-half times as long as broad; maxillary palpal segments in ratio of about 2.5:2.5:2.0:1.0, last segment often slightly shorter; minimum length of first flagellar segment equals less than one-sixth of maximum length of second segment, segments 5 to 10 with longitudinal, ventrolateral depressions (segment 4 occasionally with poorly developed depression); sternum 4 gently convex, without

median emargination; sterna 3 and 5 slightly convex medially or with apical margin transverse. Sculpturing as in female except as follows: metasomal tergum 1 with punctures extending almost to apical margin medially; terga 4 and 5 similar to tergum 3 but apical areas lacking.

Terminalia essentially as in *lupina* except as follows: sternum 7 as in *plumosa* but lateral plate with proximal lateral angle scarcely or not at all indicated, lateral margin from tip of apicolateral process to tip of apodeme forming a relatively smooth sigmoid curve; sternum 8 as in *composita;* length of gonostylus as in *plumosa* and *composita* (shorter than in *lupina*) (Figs. 64-67).

Hair: Vestiture as in female except as follows: tegulae with few brown hairs; mesoscutal dark patch smaller, rounded, about equal in size to scutellar dark patch; metasomal tergum 2 with lateral distal fasciae equal to one-fourth or less of width of tergum and reaching apical margin at extreme sides; tergum 3 with laterodistal fasciae equal to one-third or less of width of tergum; tergum 4 with distal yellow-ochre band narrowly interrupted medially or almost so by apicomedial area of dark brown hairs; tergum 5 as in tergum 4 but distal band uninterrupted; terga 6 and 7 brown medially, ochraceous to rufescent laterally; legs yellow-ochre except inner surfaces of tarsi dark red.

Remarks. Notwithstanding its broad east-west distribution (North Carolina to California), *M. coloradensis* is relatively uniform in color throughout its range. Considering again its broad range, it is somewhat surprising that *coloradensis,* a large and conspicuous bee, has been collected so sparingly.

This species is dependent upon plants of the family Compositae and, in particular, upon the genus *Helianthus* for pollen sources. In the vicinity of Lawrence, Kansas, the author was able to take *coloradensis* females gathering pollen only on *Helianthus,* although males and females were both found visiting *Vernonia* and a few other plants for nectar. Furthermore, *M. coloradensis* has been collected throughout most of its range visiting *Helianthus.* Robertson (1926) states that *coloradensis* is an oligolege of composites of the tribes Heliantheae and Cynarieae. However, if one examines records published by Robertson (1928), one finds that there are no known records of females collecting pollen on plants of the tribe Cynarieae. The few records of *coloradensis* taken on plants of the tribe Cynarieae given by Robertson (1928, pp. 65-67) involve a few specimens sucking nectar from flowers of *Cirsium* spp. There-

fore, it appears that *coloradensis* should be considered as an oligolege of the tribe Heliantheae alone, and perhaps of the genus *Helianthus.*

Type Material. Lectotype female and allotype male from Colorado are in the collection of the Academy of Natural Sciences of Philadelphia. Three female and two male paratypes from Colorado are with the lectotype.

Distribution. This species is distributed from North Carolina to California and from Wisconsin in the north to Arizona in the south (Fig. 4). It has been collected between the dates of July 2 and October 13. A total of 43 females and 37 males have been examined (including the type material) from the localities listed below. This list includes records reported in the literature.

ARIZONA: Flagstaff; Fredonia. CALIFORNIA: Canby, Modoc Co. ILLINOIS: Ashburn; Carlinville; Chicago (in vicinity of); Macoupin Co.; Peoria (at airport). INDIANA: 1 female labeled "Ind. Aug." KANSAS: Baldwin; Baldwin Junction, Douglas Co.; De Soto, Douglas Co.; Garnett; Lawrence; Lone Star Lake, Douglas Co.; Olathe; Riley Co. MISSOURI: Columbia (12 miles E.); Ozark Lake. NEBRASKA: Fairmont; Lincoln; Malcolm; Nebraska City; Omaha. NEW MEXICO: Bernalillo. NORTH CAROLINA: Cary; Raleigh. OHIO: Bowling Green (4 miles W.). UTAH: Allen's Canyon; Cornish; Greenriver; Ogden; Snowville. WISCONSIN: Milwaukee. WYOMING: Green River.

Flower Records. Cirsium sp., *C. discolor, C. lanceolatum, Coreopsis* sp., *C. tripteris, Helianthus* sp., *H. annuus, H. atrorubens, H. divaricatus, H. grosse-serratus, H. mollis, H. petiolaris, H. scaberrimus, H. tuberosus, Heliopsis helianthoides, H. laevis, Liatris pycnostachya, Lythrum alatum, Rudbeckia laciniata, Silphium* sp., *S. integrifolium, S. laciniatum, S. perfoliatum, S. terebinthinaceum, Solanum* sp., *Solidago serotina, Verbena hasta, V. stricta, Vernonia* sp., *V. baldwini interior, V. fasciculata.*

Melissodes (Callimelissodes) stearnsi Cockerell

Melissodes stearnsi Cockerell, 1905, Bull. S. California Acad. Sci., vol. 4, p. 101; 1906, Trans. Amer. Ent. Soc., vol. 32, p. 90; Linsley, 1946, Jour. Econ. Ent., vol. 39, p. 20.

Exomalopsis stearnsi Cockerell, 1906, Pomona Jour. Ent. Zool., vol. 8, p. 59; Lutz & Cockerell, 1920, Bull. Amer. Mus. N. Hist., vol. 42, pp. 567, 612.

This small distinctive bee is not closely related to any of the other members of the subgenus. The female is readily recognized by the diffuse pale pubescence on the abdominal terga and by the

abundant, long, hooked galeal hairs. The male is readily recognized by the cream-colored clypeus, the extended, hyaline, almost colorless, apical margins of sterna 3 to 5 and by the terminalia as described below.

Female. Measurements and ratios: N, 20; length, 8-11 mm.; width, 2.5-4.0 mm.; wing length, M = 2.95 ± 0.139 mm.; hooks in hamulus, M = 11.05 ± 0.160; flagellar segment 1/segment 2, M = 1.58 ± 0.019.

Structure and color: Integument as in *lupina* except as follows: clypeus often red anteromedially; metasomal terga 1-4 often dark reddish brown apically. Structure as in *lupina* except last flagellar segment longer than broad, maxillary palpal ratio about 4:3:2:1 and galeae with abundant long hooked hairs. Sculpturing as in *lupina* except as follows: clypeus with punctures large, in apical half or more elongated, in posteromedian area separated by one to two puncture widths, surface tessellate especially posteriorly; supraclypeal area impunctate medially, tessellate; vertex with flattened area posteromesad of compound eye with irregular-sized punctures separated mostly by one puncture width or more, surface unshagreened or slightly so; galeae dulled above by regular tessellation; mesoscutum with large posteromesad area impunctate, shiny, anterior third and laterally with large punctures separated by half a puncture width or less, surface shiny; scutellum with small round punctures separated by one-half to one puncture width, unshagreened; mesepisternal punctures round, deep, almost confluent, separated by one-third puncture width or less, surface dulled by dense shagreening; metasomal tergum 1 with basal half or slightly more punctate, punctures crowded basally to sparse apically, apical area impunctate, surface reticulotransversely shagreened; tergum 2 with basal area punctures separated by one-half to one puncture width, surface shiny, interband zone with punctures irregular, separated by one to two puncture widths, reticulotransversely shagreened, apical area (beneath pale pubescence) with shallow punctures separated by one-half to one puncture width, surface as in interband zone; terga 3 and 4 similar to tergum 2 but interband zone punctures distinctly smaller and more crowded.

Hair: Head pale ochraceous, yellowish on vertex. Thorax pale ochraceous laterally to yellowish on dorsum, scutellum with sparse brown hairs medially, mesoscutum with posteromedial area bare but a few brown hairs occasionally present on periphery of bare area. Metasomal tergum 1 with long pale ochraceous hairs basally

and to apical margin at extreme sides, bare apically; tergum 2 with dense white pubescence at extreme base, apical area with diffuse, appressed, short, white to subochraceous pubescence (often worn away in mediobasal part of apical area), interband zone with scattered pale pubescence and suberect pale hairs; terga 3 and 4 similar to tergum 2 but tomentum at extreme bases pale brown and interband zones with more abundant diffuse pale pubescence; terga 5 and 6 dark ochraceous medially and with white tufts at extreme sides; sternal hairs reddish brown to yellow medially, apically and laterally white. Legs pale ochraceous to white except as follows: fore tarsi, inner surfaces fore tibiae, inner surfaces middle and hind tarsi dark brown to reddish brown; scopal hairs white except brown near basitibial plates, highly plumose.

Male. Measurements and ratios: N, 20; length, 8-11 mm.; width, 2.5-3.5 mm.; wing length, $M = 2.95 \pm 0.124$ mm.; hooks in hamulus, $M = 10.45 \pm 0.209$; flagellar segment 2/segment 1, $M = 6.61 \pm 0.138$.

Structure and color: Integumental color as in *lupina* except as follows: clypeus and base of mandible cream-colored or pale yellow; metasomal terga 1-5 with apical areas subhyaline or translucent, brown. Structure as in *lupina* except as follows: eyes half as broad as long or almost so; minimum length of first flagellar segment less than one-sixth maximum length of second segment, dorsolateral depressions on segments 5 to 9 and usually extremely shallow or scarcely discernible, ultimate segment less than thrice and more than twice as long as broad, penultimate segment twice as long as broad or shorter; maxillary palpal ratio about 4.0:3.5:3.0:1.0; galeae above with abundant, extremely short, straight hairs, apical margin of sternum 4 produced into a broad, hyaline, colorless, medially emarginate flap equal in medial length to basal part of sternum or more; sterna 2 and 3 similarly produced but less so; sternum 5 with convex apical margin. Sculpturing as in female except as follows: galeae above often less intensely tessellate especially in basal third; mesoscutal posteromedial area reduced to about half of scutellum in size and occasionally with a few punctures scattered throughout; metasomal tergum 1 with punctures in basal four-fifths; terga 2 to 4 with interband zone punctures coarser than in female and apical area punctures less abundant.

Sternum 7 with median plate large, more than twice lateral plate in area (excluding neck region of median plate), apical margin forming a sigmoid curve with inner curve larger, apicolateral angle

usually folded somewhat over neck region; membranous area short and broad. Sternum 8 as in *lupina* except apex narrower and with abundant hairs at apical margin in and on each side of median emargination. Genital capsule much as in *lupina* except as follows: gonostylus short (equals half or less of gonocoxite laterally), not capitate; gonocoxite with sparse, minute spicules apically, ending in a narrow blunt process apicodorsally; spatha with apical margin scalloped, usually not emarginate medially (Figs. 68-71).

Hair: Head and thorax pale ochraceous to white. Metasomal vestiture as in female except as follows: tergum 1 with pale hairs almost to apical margin medially; terga 2-4 with diffuse pubescence of apical area usually not reaching apical margin medially (usually worn here) so that distinct bands usually present, with interband zones with less diffuse pubescence and more suberect to erect pale hairs; tergum 5 similar to tergum 4 but apical pubescence reaching medially (rarely worn away); terga 6 and 7 as in terga 5 and 6 of female; sternal hairs ochraceous to yellowish and extremely short medially to long and white or pale ochraceous laterally. Legs white to pale ochraceous except inner surfaces tarsi yellow.

Remarks. The hooked galeal hairs of the female of *M. stearnsi* are of special interest. Certain other bees, such as *Proteriades* (Michener, 1944, p. 218) and *Melissodes (Apomelissodes) apicata* (LaBerge, 1956, pp. 554-555), which have such hooked galeal hairs are seemingly oligoleges of plants whose flowers are small and tubular. The hooked hairs are an adaptation for removing pollen from these small tubular flowers.

In the case of *stearnsi* this is not so clear. This species does not appear to be highly oligolectic, although it has been collected much more frequently from various composites than from any other family of plants (see Table III). In this respect it conforms with most other species of the subgenus *Callimelissodes*. Almost half of the bees and slightly more than half of the collections of *stearnsi* in which floral data is present are from composites. However, among the 10 genera of composites recorded as being visited by this bee, no one genus is clearly preferred. Linsley (1946, p. 26) states that *stearnsi* was observed collecting pollen in several alfalfa fields in the Tracy-Patterson area of California, but was present in significant numbers in only one of these fields. Unfortunately, Linsley did not have the opportunity to study the habits of *stearnsi* nor to evaluate the importance of this species as a pollinator of alfalfa.

TABLE III. Summary of Floral Records for *Melissodes stearnsi.*

Plant Data			Floral data of *M. stearnsi*			
FAMILY	Number of genera	Number of species	Number of collections	Number of females	Number of males	Total number of bees
Compositae	10	14	33	44	38	82
Polemoniaceae	2	2	5	8	0	8
Asclepiadaceae	1	2	6	8	196	204
Leguminosae	1	1	6	2	6	8
Labiatae	1	1	4	4	2	6
Others (5)	6	6	9	5	11	16
Totals	21	26	63	71	248	319

The small size of the bee as well as the hooked galeal hairs make *stearnsi* admirably adapted for collecting pollen from the small tubular flowers of the Polemoniaceae. Females of *stearnsi* have been collected a number of times from two genera (*Hugelia* and *Gilia*) of this family. The Polemoniaceae are, generally speaking, poor collecting for an entomologist interested in bees. For these reasons, it is tempting to predict that *stearnsi* will be found to be an oligolege on plants of the family Polemoniaceae and that the present collections do not support this hypothesis because the phloxes are not as assiduously searched for bees by entomologists as are other plants, such as the composites.

Another hypothesis which could lead to interesting evolutionary speculation is that *M. stearnsi* evolved as an oligolege of such plants as the Polemoniaceae, but has subsequently become more diversified in its pollen-source preferences. Additional collections with serious study of the habits of this bee in nature are needed to resolve these questions.

Type Material. Holotype female of *stearnsi* from Los Angeles, California, collected by Davidson is in the collection of P. H. Timberlake at the Citrus Experiment Station, Riverside, California.

Distribution. This species is distributed from southern California to Washington and is, by far, most abundant in California (Fig. 8).

It has been taken between the dates of March 4 and October 12 but mainly during the months of June to August. A total of 264 females and 431 males, including the holotype, have been examined from the localities listed below (including records from the literature).

California: Alpine; Antioch; Arroyo Seco, Monterey Co.; Artois; Auburn; Bass Lake, Modoc Co.; Calistoga; Chico; Claremont; Clear Lake; Clovis (4 miles N.); Coalinga (7 miles N. W.); Covina; Davis; Dos Palos; Dutch Flats, Placer Co.; Elsinore; Fresno; Friant; Galt; Glen Ivy; Hamilton City; Hemet; Hopland Field Station, Mendocino Co.; Jamesburg (Hastings Natural History Reservation); Knoxville; Lindsay; Los Angeles; Los Angeles Co.; Los Banos; Masourka Canyon, Inyo Mts.; Mendocina Co.; Mix Canyon, Solano Co.; Mokelumna Hill; Mt. Diablo, Contra Costa Co.; Mt. Santiago; Murphys; Murrieta; Nelson; Ojai (7.8 miles W.); Orland; Oroville; Palmdale (Mohave Desert); Palo Alto; Pasadena; Patterson; Pillsbury Lake, Lake Co.; Poway; Puente; Puente Hills; Putah Canyon, Solano Co.; Rawhide; Redding; Riverside; Romaland; Ryer Island, Solano Co.; San Dimas; San Gabriel Mts. (near Pasadena); Santa Clara Co.; Santa Cruz Co.; Spreckels; Stockton; Sunset Valley, Santa Barbara Co.; Temecula; Tollhouse; Topanga Canyon; Tracy; Tuckers Grove; Turlock; Visalia; Vista; Watts Valley; Westley; Westwood Hills, Los Angeles Co.; Whittier; Willows; Winters; Woodlake; Yorba Linda. Oregon: Butte Falls (7 miles W.); Lane-Benton Park (20 miles S. of Corvallis); Medford. Washington: Colokum Pass.

Flower Records. Althaea rosea, Asclepias sp., *A. eriocarpa, Aster* sp., *A. exilis, Brassica* sp., *Centaurea solstitialis, Centromadia* sp., *C. pungens, Cirsium* sp., *Cleome* sp., *Corethrogyne* sp., *C. bernardense, C. virgata, Datura* sp., *D. metaloides, Eremocarpus setiger, Ericameria palmeri, E. parishii, Eriogonum* sp., *E. setiger, Gilia virgata, Gutierrezia* sp., *G. californica, G. sarothrae, Helianthus* sp., *H. annuus, Heliotropium curassavicum, Hemizonia* sp., *H. fasciculata, Hugelia virgata, Medicago sativa, Silybum marianum, Trichostema* sp., *T. lanceolatum.*

Subgenus *Eumelissodes* LaBerge

Eumelissodes LaBerge, 1956, Univ. of Kansas Sci. Bull., vol. 37, p. 1177. Type species: *Melissodes agilis* Cresson, by original designation.

This subgenus has been described in detail by LaBerge (1956, p. 1177). A brief diagnosis is given here with a few additional characteristics added.

Female. Clypeus flat to gently protuberant, never protruding beyond eye in profile by as much as half width of eye; galeae smooth and shiny to variously shagreened or tessellate, less than twice and usually less than one and one-half times as long as median clypeal length; maxillary palpi 4-segmented; last flagellar segment always longer than broad, second flagellar segment usually slightly broader than long, but occasionally as long as broad or slightly longer. Metanotum usually shorter than dorsal surface of propodeum medially, rarely longer; propodeum with dorsal surface rarely punctate apically and then punctures small and obscured by tessellation, reticulorugose basally. Metasomal tergum 7 with gradulus with lateral parts absent or cariniform and short, never lamelliform or long.

Vestiture variable; thorax and tergum 2 without spatuloplumose hairs; terga 2-4 never with apical pale bands subequal to each other in length and subequal in length across each tergum, that of tergum 2 usually narrowly interrupted medially; scopal hairs usually highly plumose, never simple.

Male. Clypeus entirely pale to entirely black in color; labrum often all dark-colored, usually with mediobasal pale spot, rarely entirely pale but often mostly pale except for narrow brown apical margin; mandibles often with basal yellow spots. Minimum length first flagellar segment always less than half maximum length second segment and usually less than one-third second segment. Sterna 3-5 with apical margins slightly but distinctly concave or straight, never broadly convex or produced into a bilobed flap. Gonostylus usually somewhat capitate, often not, half as long as gonocoxite or longer in dorsal view, slender, usually less than half as wide as greatest width of penis valve, with short hairs near base and often on outer surfaces; sternum 7 with median plate large, flat, transparent, with abundant hairs ventrally; lateral plate usually piceous at least apically, with distinct apical or apicolateral process, greater than one-third median plate in area. Other structural characters as in female.

Vestiture as in female but tergum 5 often with pale band similar to that of tergum 4; terga 6 and 7 often with pale hairs.

KEY TO THE SPECIES OF THE SUBGENUS EUMELISSODES

MALES

1. Metasomal terga usually with no complete pale pubescent bands, *if* at most one complete band present (tergum 2), *then* labrum all or almost all black and thorax with ferrugineous to rufous hairs ..... *dentiventris* Smith

   Metasomal terga 2-5 usually all with pale distal band, *if* only one complete band present, *then* not on tergum 2 *or* labrum with large yellow spot and/or thoracic hairs not ferrugineous, often partly brown 2

2 (1). Labrum wholly light-colored (without narrow brown apical margin); mandible with a large basal pale spot, *verbesinarum* Cockerell (in part)

   Labrum usually at least margined with dark and mandible often without light basal spot 3

3 (2). Penultimate flagellar segment less than three times as long as wide (narrowest width and maximum length); flagellum in repose not surpassing pterostigma 4

   Penultimate flagellar segment three times as long as broad or longer and/or antennae in repose surpassing pterostigma .. 10

4 (3). Labrum and bases of mandibles black; propodeum with dorsal surface with small, round, discrete punctures laterally of about same size as on scutellum; metasomal tergum 1 with short, appressed, simple brown hairs apically, *paucipuncta*, n. sp.

   Labrum and bases of mandibles black or with yellow spots; propodeum with dorsal surface reticulorugose, at least basally, punctures when present elongate; metasomal tergum 1 with long erect or suberect hairs reaching or almost reaching margin 5

5 (4). Penultimate flagellar segment twice as long as wide or shorter; maximum length first flagellar segment about half as long as maximum length second segment, *monoensis*, n. sp.

   Penultimate flagellar segment longer than twice width; maximum length first flagellar segment less than half as long as second 6

6 (5). Labrum and bases of mandibles black, without yellow spots; antennae in repose reaching pterostigma 7

   Labrum and often mandibles marked with yellow; antennae in repose often not reaching pterostigma 8

7 (6). Metasomal terga 2 and 3 with interband zones with surfaces dulled by fine, dense, reticulotransverse shagreening; minimum length first flagellar segment usually equals one-third or more maximum length second segment, *grindeliae* Cockerell (in part)

   Metasomal terga 2 and 3 with interband zones with surfaces shiny, unshagreened, minimum length first flagellar segment equals less than one-third maximum length second segment ..... *hymenoxidis* Cockerell

8 (6). Mandibles with basal yellow maculae, *pallidisignata* Cockerell (in part)
Mandibles without basal yellow maculae 9

9 (8). Terga 2-5 with apical areas opaque, deep reddish brown; terga 4-6 with basal areas covered with reddish brown hairs and pubescence ..... *rustica* (Say) (in part)
Terga 2-5 with apical areas hyaline, colorless to testaceous or yellowish brown; terga 4-6 with basal areas with pale pubescence and hairs ..... *pallidisignata* Cockerell (in part)

10 (3). Mesoscutal and scutellar punctures minute, mesoscutum with large posteromedian area impunctate or with scattered punctures less than ⅓ mesepisternal punctures in diameter, mesoscutal punctures anteromedial to parapsidal lines no larger and usually smaller than mesepisternal punctures and separated mostly by 2 to 3 puncture widths or more, *expolita*, n. sp.
Mesoscutal and scutellar punctures larger and more abundant, posteromedial mesoscutal area with scattered punctures as large as or larger than mesepisternal punctures, area anteromedial to parapsidal lines with punctures at least as large as mesepisternal punctures and usually separated by one puncture width or less 11

11(10). Metasomal terga with apical areas deeply infumate, completely opaque or almost so; clypeus yellow except apical margin and spots or notches at anterior tentorial pits 12
Metasomal terga with apical areas transparent, colorless or slightly infumate and translucent, not opaque; *if* infumate and opaque or almost so, *then* with clypeus black or partially black 30

12(11). Minimum length first flagellar segment equals ⅐ or less of maximum length second segment and usually no longer than pedicel on the same side; terga 2 and 3 often with distinct punctures in apical areas 13
Minimum length first flagellar segment equals more than ⅐ of maximum length of second segment, distinctly longer than pedicel on same side; terga 2 and 3 usually with apical areas impunctate 27

13(12). Clypeus white or creamy anteriorly with black extending down from face onto posterior part; without pale spots on bases of mandibles; galeae densely tessellate, *denticulata* Smith (in part)
Clypeus all pale except spots or notches at tentorial pits and anterior margin, or *if* black extends down from face onto posterior part of clypeus, *then* pale portion bright yellow, not whitish; mandibles often with pale basal spots; galeae variable, may be tessellate 14

14(13). Basitibial plate with apical margin straight and at right angles to posterior margin; apical area of tergum 2 with small piliferous punctures; minimum length first flagellar segment usually 1/10 maximum length second segment or less, *manipularis* Smith

Basitibial plate rounded apically, *if* somewhat truncate, *then* apical area tergum 2 without piliferous punctures; shortest length first flagellar segment usually slightly longer than 1/10 of longest length second segment 15

15(14). Clypeus all pale except spots or notches at tentorial pits and anterior margin, *if* narrowly infuscated posteriorly, *then* hairs on mesonotum anterior to patch of dark hairs white to pale ochraceous, *or* mesoscutum without dark hairs; mandibles often with pale basal spots 16

Clypeus not all pale, infuscated posteriorly at least; hairs on mesoscutum anterior to dark patch fulvous or ferrugineous; mandibles without yellow basal spots 25

16(15). Clypeus white or cream-colored, about same color as pale spot on labrum; spots at base of mandibles white; with piliferous punctures in marginal areas terga 2 and 3, *pilleata,* n. sp.

Clypeus yellow, usually more brightly colored than pale labral spot if the latter is present; basal mandibular spots yellow, if present; *if* the above areas cream-colored, *then* without piliferous punctures in apical areas terga 2 and 3 17

17(16). Hairs of thorax pale to bright ferrugineous, without dark hairs on mesoscutum or scutellum; metasomal tergum 3 with apical area with few or no piliferous punctures although dark brown hairs may be present..... *trinodis* Robertson

Thorax with hairs ochraceous to white *and/or* large dark mesoscutal patch present; *if* dark hairs absent on mesoscutum and scutellum, *then* apical area tergum 3 with minute piliferous punctures 18

18(17). Posterior surfaces hind basitarsi with hairs as long as tibial spurs and tibiae with hairs as long as tibial spurs or almost so; sterna with interpunctural surface shiny, unshagreened ..... *interrupta,* n. sp.

Posterior surfaces hind basitarsi with hairs much shorter than tibial spurs; sterna often with interpunctural surfaces dulled by reticular shagreening; tibial hairs shorter than tibial spurs 19

19(18). Thorax with hairs posterior to dark brown patch ferrugineous; first metasomal tergum with small punctures separated by much more than one puncture width and usually 2 or 3, with apical area with dark brown or black hairs in narrow band medially and widening into two lateral lobes extending back more than one-half width of dorsum of tergum at sides; terga 2 and 3 with abundant brown hairs apically, but these not arising from distinct punctures 20

Thorax with hairs posterior to dark brown patch pale, not ferrugineous; first metasomal tergum with punctures more closely spaced, with apical area without dark brown hairs or these not arranged in narrow band medially and two lateral lobes; terga 2 and 3 without dark hairs apically or these arise from distinct punctures; or not with all of these characters combined..... 21

20(19). Terga 2-4 with interband zones impunctate or almost so, dulled by fine, dense tessellation; labrum and usually bases of mandibles with pale spots ..... *wheeleri* Cockerell

Terga 2-4 with abundant round punctures in interband zones, surface with weak tessellation; labrum and bases of mandibles without pale spots, black ..... *pullata* Cresson

21(19). Mesoscutum and scutellum with abundant dark brown or black hairs; mesepisterna usually roughened by coarse shagreening; terga 2 and 3 with apical areas impunctate or indistinctly so 22

Mesoscutum and usually scutellum without dark hairs (occasionally present on both); mesepisterna with surface usually smooth and shiny, lightly shagreened if at all; terga 2 and 3 with apical areas with piliferous punctures 23

22(21). Minimum length first flagellar segment usually equals ⅛ to 1/9 maximum length second segment; galeae usually shiny above, lightly shagreened or not at all except near tips, *illata* Lovell and Cockerell

Minimum length first flagellar segment 1/7 or more of maximum length of second segment, never as little as ⅛; galeae above usually shagreened at least in apical half, rarely shiny and unshagreened ..... *subillata*, n. sp. (in part)

23(21). First metasomal tergum with long, white or pale ochraceous, barbed, subappressed hairs in apical area ..... *elegans*, n. sp.

First metasomal tergum medially with short, relatively simple, appressed, brown to black hairs in apical ¼ or more 24

24(23). First metasomal tergum more coarsely punctate; terga with apical areas dark brown, only slightly translucent; mesepisterna coarsely punctate ..... *boltoniae* Robertson

First metasomal tergum less coarsely punctate; terga usually with apical areas pale brown and translucent to transparent; mesepisterna less coarsely punctate ..... *fumosa*, n. sp.

25(15). Clypeus flat, with deep, round punctures as large as those on supraclypeal area ..... *elegans*, n. sp. (in part)

Clypeus strongly bowed out, with small, indistinct punctures obscured by dense shagreening 26

26(25). Mesoscutum and scutellum and usually tegulae with dark brown hairs; clypeus usually half black or more, *tincta*, n. sp.

Mesoscutum and scutellum with few or no dark hairs, no dark hairs on tegulae; clypeus with very narrow posterior margin infuscated, if at all ..... *trinodis* Robertson (in part)

27(12). Terga 2 and 3 with apical areas (just apical to pale pubescent band) with large, distinct punctures, 3 or 4 times as broad as bases of hairs arising from them; terga 3 and 4 with interband zones opaque, dulled by small, dense tessellation; galeae shiny above, unshagreened except near tips; mesoscutal hairs long, pale ..... *fasciatella*, n. sp.

Terga 2 and 3 with apical area without distinct punctures or

these minute; terga 3 and 4 with interband zones shiny or moderately shiny, *if* finely tessellate and opaque, *then* galeae dulled above by dense shagreening in at least apical half 28

28(27). Hairs of mesoscutum and scutellum ferrugineous, no dark brown or black hairs; tergum 5 with pubescence brown at least medially ..... *bidentis* Cockerell

At least scutellum with some dark brown or black hairs and often mesoscutum as well, *if* without dark hairs, *then* mesoscutal hairs pale ochraceous or cinereous; pubescence of tergum 5 usually pale 29

29(28). Terga 2-4 with apical areas no wider than or very slightly wider than pale distal bands on those segments; terga 2-5 with apical areas shiny, only delicately shagreened, often with a few piliferous punctures basally and laterally, usually reddish brown in color ..... *rustica* (Say) (in part)

Terga 2-4 with apical areas as wide or wider than width of pale distal band on those segments; terga 2-5 with apical areas usually black, opaque, dulled by dense reticular shagreening, with no piliferous punctures but often with short, simple, appressed, dark brown hairs *subillata*, n. sp. (in part)

30(11). Hind legs with hairs short, tibiae with mid-outer surfaces with hairs mostly ⅔ as long as maximum width of tibiae or less; galeae dulled above by dense, regular tessellations; pale areas of clypeus white or cream-colored 31

Hind legs with longer hairs, tibial mid-outer surface with hairs mostly longer than ⅔ maximum width of tibiae; galeae variously sculptured; pale areas of clypeus usually yellow, 32

31(30). Terga 2 and 3 with interband zones with distinct punctures, especially laterally and beneath distal pale band, surfaces relatively shiny, reticular shagreening present but not so dense as to make surface opaque; clypeus darkened posteriorly; mandible without pale basal spot; terga 2-5 with apical areas usually piceous or at least infumate, *denticulata* Smith (in part)

Terga 2 and 3 with interband zones with few or no punctures, when present punctures small, shallow, indistinct, surfaces dulled by dense reticular shagreening; clypeus usually entirely pale; base of mandible usually with pale spot; terga 2-5 usually with apical margins hyaline, colorless to slightly yellowed ..... *vernoniae* Robertson

32(30). Maximum length first flagellar segment equal to more than ⅓ minimum length *third* flagellar segment 33

Maximum length first flagellar segment equals ⅓ or less minimum length *third* flagellar segment 39

33(32). Wing veins yellow to red; galeae shiny, unshagreened above; terga 2-5 with interband zones impunctate or with punctures minute (scarcely wider than bases of hairs arising from them) and obscured by dense shagreening; mandible

without yellow spot at base; labrum with or without pale median spot ..... *perlusa* Cockerell (in part)

Wing veins brown or reddish brown, *or, if* yellow, *then either* terga 2-5 with distinct punctures in interband zones, *or* mandible with basal yellow spot, *or* galeae dulled by shagreening above 34

34(33). First metasomal tergum with distinct distal band of long, dense, appressed or subappressed, white hairs reaching apical margin and obscuring apical hyaline zone across entire tergum (occasionally worn) 35

First metasomal tergum without apical band of dense white hairs or these restricted to lateral patches each ⅓ width of tergum or less, or, *if* present across tergum, *then* not obscuring surface medially 37

35(34). Base of mandible with yellow spot; labrum yellow with dark border; minimum length first flagellar segment usually equals ⅓ or more maximum length *third* segment 36

Base of mandible black; labrum black or with small mediobasal pale spot; minimum length first flagellar segment usually equals less than ⅓ maximum length third segment, *bimatris,* n. sp.

36(35). Mesoscutum with posteromedian area punctures separated mostly by more than one puncture width, *semilupina* Cockerell

Mesoscutum with punctures of posteromedian area separated mostly by less than one puncture width ..... *ochraea,* n. sp.

37(34). Mandible usually without basal pale spot, *if* pale spot present, *then* mesoscutum and scutellum with black hairs medially; galeae with surfaces dulled by dense shagreening, *robustior* Cockerell

Mandible with basal yellow spot and mesoscutum without black or dark brown hairs, *or* galeae with surface shiny, not dulled by shagreening 38

38(37). Labrum and mandibular bases with yellow; mesoscutum and scutellum without dark hairs medially, *menuachus* Cresson (in part)

Labrum and mandibular bases without pale spots; mesoscutum and scutellum often with abundant dark hairs medially ..... *grindeliae* Cockerell (in part)

39(32). Clypeus all or partially black 40

Clypeus all light-colored except anterior margin and notches or spots at tentorial pits 54

40(39). Clypeus usually partly yellow; flagellar segments with flattened or depressed area laterodorsally, this area shiny; galeae shiny above, unshagreened except at tips; terga with apical areas opaque, dark reddish brown to black, *paulula,* n. sp.

Clypeus partly or wholly black; flagellar segments not depressed or flattened laterodorsally, or, if so, then flattened areas not shiny; galeae variable, often shagreened or tessellate above; terga various, but often hyaline apically.... 41

41(40). Clypeus entirely black; without black or dark brown suberect hairs on terga 2-7; clypeus often with small median shiny boss; antennae extremely long, usually last segment or two darker than preceding segments; body vestiture generally white ..... *tristis* Cockerell (in part)

Clypeus usually with some yellow or whitish marking, *if* entirely black, *then either* terga with some dark brown or black, erect or suberect hairs (especially in apical areas of terga 2 and 3 or in interband zones of terga 3-5), *or* body vestiture yellowish and last segments of antennae not darker than preceding segments 42

42(41). Clypeus entirely black; galeae dulled by fine dense tessellation, with at least longer hairs on basal half hooked or bent near tips; last 5 or 6 flagellar segments nodose, *melanura* Cockerell

Clypeus not entirely black, or *if* all black, *then* galeae shiny or only slightly shagreened, not tessellate and without hooked hairs; flagellar segments usually not nodose 43

43(42). With black or brown hairs on vertex between the eyes 44

Without black or brown hairs on vertex of head 50

44(43). Last two flagellar segments entirely black, preceding segments yellow to red, or dark only below; galeae lightly shagreened, shiny, with long hairs hooked near tips, *terminata*, n. sp.

Last two flagellar segments not contrasting sharply with preceding segments in color; galeae various, usually without hooked hairs 45

45(44). Metasomal terga with apical areas deeply infumate 46

Terga with apical areas hyaline, only slightly infumate at most 47

46(45). Galeae with long hairs dorsally some of which are bent or hooked near tips ..... *moorei* Cockerell

Galeae with short, straight hairs dorsally ..... *exilis*, n. sp.

47(45). Last exposed sternum with strong oblique lateral lamelliform carinae as high as apical area of sternum just posterior to each carina, at least twice as long as gap between carinae and with area between carinae dulled by punctation and dense, irregular shagreening ..... *micheneri*, n. sp.

Last exposed sternum with oblique lateral carinae weak, not high and sharp, less than twice as long as gap between their apices; area between carinae at least partly shiny .. 48

48(47). Clypeus entirely black; first flagellar segment at base distinctly narrower than width of median ocellus (measure flagellar segment at extreme base in lateral view); metasomal tergum 2 with distal white pubescent band well-separated from margin of tergum by zone of short, appressed, simple, black or dark brown hairs .... *personatella* Cockerell

Clypeus usually not all black, *if* all black, *then* first flagellar segment laterally at base at least as broad as median ocellus and usually broader; tergum 2 with distal pale band arched, usually reaching apex laterally, often interrupted, 49

49(48). Shortest length first flagellar segment usually equals ⅓ or less of longest length second segment; flagellar segments entirely black except small ventral pale spot; small bees 8 to 12 mm. in length ..... *microsticta* Cockerell

Shortest length first flagellar segment often equals more than ⅓ longest length second segment; antennae usually not entirely black, or if so, then not with pale spots ventrally; larger bees, 11 to 14 mm. in length 51

50(43). Flagellar segments 5-10 nodose; minimum length first flagellar segment more than ⅛ maximum length second segment ..... *hurdi*, n. sp.

Flagellar segments 5-10 not nodose; minimum length first flagellar segment equals ⅛ or less of maximum length second segment 51

51(49, 50). Tergum 2 with depressed area at extreme base (under edge of tergum 1 unless untelescoped) with coarse, round punctures separated mostly by one puncture width or less; antennae never entirely black, usually red at least below.. 52

Tergum 2 with depressed area at extreme base with minute, round punctures separated by more than one puncture width and often by 2 or 3 puncture widths or more; antennae often entirely black or dark brown..... 53

52(51). Pale head and thoracic hairs white; clypeus with surface dulled by dense transverse shagreening, *gelida*, n. sp. (in part)

Pale head and thoracic hairs ochraceous to pale fulvous; clypeus shiny or moderately shiny, shagreening absent or sparse and coarse 86

53(51). Clypeus with surface dulled by dense reticular shagreening; supraclypeal area dulled by dense reticular shagreening; mesepisterna with surfaces usually with delicate, sparse shagreening; Baja California ..... *comata*, n. sp.

Clypeus and supraclypeal area often with surfaces shiny, unshagreened; mesepisterna without shagreening; United States and Mexico ..... *confusa* Cresson

54(39). Pygidial plate broader at extreme base than median length; mandible black basally, labrum cream-colored with black apical margin; galeae shiny, unshagreened; wing veins yellow or red; head and thorax without black hairs, *brevipyga*, n. sp.

Pygidial plate as long as width at base or longer, *if* broader at base than long (rare), *then either* mandible yellow at base, *or* labrum all black, *or* galeae dulled by shagreening, *or* wing veins brown to black; vertex, mesoscutum and/or scutellum often with dark hairs 55

55(54). Labrum largely or wholly white or cream-colored, more than 0.6 times as long as broad; pygidial plate narrow, ⅔ or less as broad at base as long; mandible with basal yellow spot; galeae shiny, unshagreened except at tips; wing veins dark

brown; vertex of head, thorax and terga often with dark brown hairs ..... *velutina* (Cockerell)

Labrum entirely black, or 0.6 times as long as broad or shorter, *or* pygidial plate more than ⅔ as broad as long, *or* galeae dulled by shagreening, *or* mandibles without yellow spots, *or* wing veins pale; head, thorax and metasomal terga with or without dark hairs; not with the combination given above 56

56(55). Minimum length first flagellar segment half as long as its own maximum length and no longer than pedicel on that side; galeae shiny above, without shagreening except near tips; metasomal tergum 2 with pale pubescent band less than half as wide medially as apical area; terga 2 and 3 with interband zones dulled by dense shagreening, impunctate or punctures shallow and obscured by shagreening; apical areas terga 2-5 dulled by dense, fine reticular shagreening 57

Minimum length first flagellar segment equals more than half maximum length first segment and longer than pedicel on same side, *if* short, *then either* with galeae dulled by shagreening, or tergum 2 with pale band broader than half of apical area, *or* terga 2 and 3 with interband zones shiny or moderately so with distinct punctures; apical areas of terga 2-5 usually moderately shiny to shiny 59

57(56). Mandible usually with small yellow basal spot; clypeus dulled by transverse shagreening in interpunctural areas, punctures small; labrum with pale mediobasal spot, *gelida*, n. sp. (in part)

Mandible without basal yellow spot; clypeus shiny to moderately so, with no or little shagreening dulling surface, punctures coarse; labrum with or without pale spot 58

58(57). Medium-sized to large bee, 12-14 mm. in length; tergal apices usually yellow; tergum 1 with apical hairs thickly plumose; minimum length first flagellar segment usually equals ⅐ or more maximum length second segment, *submenuacha* Cockerell (in part)

Small to medium-sized bees, 9-13 mm. in length; tergal apices usually colorless; tergum 1 with apical hairs sparse, not thickly plumose; minimum length first flagellar segment usually equals less than ⅐ maximum length second segment ..... *coreopsis* Robertson

59(56). Metasomal terga 2 and 3 with interband zones with deep punctures of irregular size but many as large and almost as deep as mesoscutal punctures; terga 3 and 4 with basal depressed areas with punctures fully as large and deep as mesoscutal punctures; apical areas of terga smooth, shiny, impunctate; last exposed sternum coarsely punctate; mandible and labrum black; galeae shiny above, unshagreened, *perpolita*, n. sp.

Metasomal terga 2 and 3 with interband zones variously punctured but punctures not nearly as large as mesoscutal punctures; terga 3 and 4 with basal areas with punctures much smaller than mesoscutal punctures; apical areas variously punctate; last exposed sternum usually not coarsely punctate; mandibles, labrum and galeae various; not with the combination of characters given above 60

60(59). Mandible with basal yellow spot *and* labrum with large mediobasal pale spot (as large as ⅓ area of labrum and usually larger) 61

Mandible without yellow basal spot *and* labrum with or without pale mediobasal spot (rarely both mandible and labrum with pale spots, but then pale labral spot equals less than ⅓ of area of labrum and/or mandibular spots minute; also rarely with labrum black and mandible with minute yellow spot) 68

61(60). Galeae dulled above by fine reticular shagreening; wing veins red to yellow; hairs of head and thorax usually pale ferrugineous or at least ochraceous . . . . . *agilis* Cresson

Galeae shiny above, not dulled by shagreening except at tips, *or, if* shagreened, *then* either wing veins brown to black or head and thoracic hairs white or with some dark brown admixed 62

62(61). Flagellar segment 1 with maximum length equal to about or almost ⅓ maximum length flagellar segment 3, with minimum length segment 1 much longer than pedicel on same side; large bee, 12-15 mm. in length, *menuachus* Cresson (in part)

Flagellar segment 1 with maximum length equal to much less than ⅓ maximum length flagellar segment 3, with minimum length scarcely, if at all, exceeding length of pedicel on same side; small to medium-sized, 8-13 mm. in length . . 63

63(62). Tergum 2 with distal pale band as broad or broader than apical area medially; clypeus with large deep punctures, surface usually shiny, unshagreened; thoracic hairs above usually very pale ochraceous 64

Tergum 2 with distal pale band narrower than apical area medially, *or, if* about as broad, *then* clypeus with shallow punctures and surface dulled by fine shagreening; thoracic hairs usually white 66

64(63). Pygidial plate as broad at base as long or slightly broader; mesoscutum with posteromedian area with punctures crowded, separated mostly by half a puncture width or less . . . . . *pexa,* n. sp.

Pygidial plate narrower than long and/or mesoscutal punctures less crowded, separated mostly by more than half a puncture width 65

65(64). Mandible with basal yellow macula large, almost forming a complete band across base of mandible; tergum 1 with

plumose hairs obscuring apical margin, extremely dense and highly branched..... *verbesinarum* Cockerell (in part)

Mandibular basal yellow spot small, distinctly triangular; tergum 1 with apical band less dense and hairs less branched ..... *humilior* Cockerell

66(63). Wing veins all pale, yellow to orange; galeae often with delicate, reticular shagreening above..... *snowii* Cresson

Wing veins red to brown (especially forewings), *if* mostly pale, at least subcostal vein and pterostigma reddish brown; galeae usually shiny, unshagreened above..... 67

67(66). Terga 2-5 with apical areas always colorless, hyaline; terga 6 and 7 often with brown hairs; terga 2-4 often with hairs of interband zones yellow to brown, *verbesinarum* Cockerell (in part)

Terga 2-5 with apical areas often infumate; terga 6 and 7 with hairs white to yellow; terga 2-4 with hairs of interband zones white..... *nivea* Robertson

68(60). Vertex, tegulae, mesoscutum and scutellum with abundant dark brown hairs, and/or antennae wholly dark brown to black 69

Tegulae without dark hairs, vertex with few or no dark hairs, mesoscutum and scutellum usually without dark hairs; antennae always at least red below and dark above, often wholly pale 70

69(68). Tergum 2 with depressed basal area with large round punctures separated mostly by one puncture width or less; flagellar segments always pale at least below, *montana* Cresson (in part)

Tergum 2 with basal depressed area with punctures minute and separated mostly by 2 or more puncture widths; flagellar segments often entirely dark brown or black, *confusa* Cresson (in part)

70(68). Metasomal tergum 1 with apical ¼ to ⅓ medially with short, relatively simple, brown to black, appressed to subappressed hairs; terga 2-5 often with apices slightly or deeply infumate 71

Metasomal tergum 1 with apical ¼ to ⅓ medially with long, relatively plumose, white or pale ochraceous hairs, or bare; apical areas terga 2-5 usually colorless, rarely slightly infumate 73

71(70). Galeae usually dulled by dense tessellation above; hairs of posterior basitarus along posterior margin much shorter than tibial spurs ..... *fumosa,* n. sp. (in part)

Galeae shiny, unshagreened except at tips and laterally; hairs posterior of hind basitarsus often as long as tibial spurs or longer 72

72(71). Tergum 2 with distal pale band narrowly interrupted medially; hind basitarsus with hairs of posterior margin distinctly longer than tibial spur ..... *interrupta,* n. sp. (in part)

Tergum 2 with distal pale band not interrupted medially (unless worn); hairs along posterior margin hind basitarsus no longer than tibial spur or shorter, *montana* Cresson (in part)

73(70). Length forewing plus tegula equals 1.0 cm. or more, large bees; tergum 1 with apical area obscured by several rows of short, highly plumose, appressed hairs; tergum 2 with apical ⅜ or more hyaline, yellowish; terga 2-4 with interband zones impunctate or punctures minute and obscured by dense shagreening; first flagellar segment equals little more than pedicel on same side; wing veins red, *submenuacha* Cockerell (in part)

Medium-sized to small bees, length forewing plus tegula less than 1.0 cm.; tergum 1 with apical area not hidden by plumose hairs; tergum 2 usually with apical hyaline area equal to less than ⅜ length of tergum, usually colorless; terga 2-4 with interband zones with distinct punctures *or* wing veins reddish brown to black 74

74(73). Minimum length first flagellar segment no longer (or scarcely longer) than pedicel on that side, half as long as maximum length and ⅛ or less as long as maximum length segment 2; galeae unshagreened above; labrum usually entirely black; tergum 2 with minute punctures separated by 3 or more puncture widths in interband zone; tergum 2 usually with brown hairs in interband zone and often in apical area as well ..... *limbus*, n. sp.

Minimum length flagellar segment 1 usually distinctly longer than pedicel on that side, usually longer than half maximum length, and greater than ⅛ maximum length segment 2; galeae often shagreened above; labrum often with pale median spot; tergum 2 with punctures and hair color variable, but not with combination of characters given above.. 75

75(74). Tergum 2 with punctures of interband zone minute, separated mostly by 3 puncture widths or more, scarcely broader than bases of hairs arising from them; terga 3 and 4 with punctures of interband zones minute to small, separated mostly by about 2 puncture widths (often less on tergum 4), indistinct and shallow 76

Tergum 2 with interband zone punctures larger, separated mostly by 2 or less puncture widths, distinctly broader than bases of hairs arising from them; terga 3 and 4 with large, round, deep punctures separated mostly by 1 puncture width; *or if* terga 2, 3 and 4 with minute well-separated punctures, *then* wing veins yellow to red and bee of medium size 77

76(75). Labrum usually without pale median spot or spot less than ⅓ of area of labrum; galeae dulled by dense reticular shagreening above; pygidial plate broad, width usually more than ⅔ length ..... *utahensis*, n. sp.

Labrum with pale median spot and spot usually equals ½ or more of area of labrum; galeae shiny above, unshagreened except at tips; pygidial plate usually narrow, width usually equals less than ⅔ length and often as little as ½ of length, *vernalis*, n. sp.

77(75). Terga 2-4 with interband zones impunctate or with minute punctures scarcely broader than bases of hairs arising from them, separated by 2 to 4 puncture widths, surface dulled by fine tessellation; wing veins red; galeae shiny above except at tips ..... *perlusa* Cockerell (in part)

Terga 2-4 with interband zones with distinct punctures separated mostly by one puncture width or less (especially on terga 3-4), surface shiny or dulled by reticular shagreening; wing veins yellow to dark brown; galeae shiny or dull, shagreened or unshagreened 78

78(77). Pygidial plate broader at base than median length; wing veins brown to reddish brown; galeae shiny, unshagreened above except at tips; dorsum of thorax with hairs yellow; tergal vestiture ochraceous; tergum 2 with interband zone punctures deep, round, separated mostly by less than one puncture width ..... *relucens*, n. sp.

Pygidial plate at least as long as broad and usually longer, *if* broader at base than long, *then* wing veins yellow to red *or* galeae dulled by fine shagreening above; hairs of thorax and terga various in color; tergum 2 with interband zone punctures usually separated by about one puncture width 79

79(78). Flagellar segment 1 with minimum length equal to ⅛ or less of maximum length segment 2 and scarcely longer than pedicel on same side; galeae often shagreened at least on apical halves above; labrum with mediobasal pale spot; terga 2-5 with apices often infumate, yellowish brown to yellow 80

Flagellar segment 1 with minimum length equal to more than ⅛ and usually more than ⅐ maximum length segment 2, usually distinctly longer than pedicel on same side; labrum with or without pale spot; galeae often shiny, unshagreened; tergal apices usually colorless 81

80(79). Tergum 2 with interband zone with erect to suberect, long, white hairs ..... *elegans*, n. sp. (in part)

Tergum 2 with interband zone with erect to suberect, short, brown hairs ..... *fumosa*, n. sp. (in part)

81(79). Terga 2-5 with at least some of the erect hairs of interband zones brown or black and often with some or all of suberect hairs of apical areas brown as well; veins of hind wing, as well as fore wing, usually dark reddish brown to black; medium-sized bees, hamuli usually with 12 or more hooks ..... *montana* Cresson (in part)

Terga 2-5 with erect hairs of interband zones and suberect

hairs of apical areas (when present) ochraceous or white; veins of hind wings often red to yellow; small to medium-sized bees, hamuli often with 11 or fewer hooks 82

82(81). Tergum 1 with apical hairs short, appressed, white, dense and plumose so that a distinct white band is formed across entire tergum; tergum 2 with distal pale band at least as broad as apical apubescent area and usually broader; occasionally with brown hairs on mesoscutum and scutellum 83

Tergum 1 with apical hairs dense and plumose only laterally, if at all, medially with hairs sparse and/or barbs minute; tergum 2 with distal pale band often narrower than apical area; dorsum of mesoscutum and scutellum without dark hairs 84

83(82). Scutellum with brown hairs (at least a few) and mesoscutum often with brown hairs; galeae often dulled by delicate shagreening above ..... *lutulenta*, n. sp.

Mesoscutum and scutellum without brown hairs; galeae shiny above, not shagreened except at tips ..... *appressa*, n. sp.

84(82). Head and body hairs long, those of middle of vertex (head in facial view) mostly longer than flagellar segment 3; galeae shiny above, unshagreened except at tips; vestiture ochraceous; Mexico ..... *rufipes*, n. sp.

Head and body hairs shorter, those of middle of vertex mostly shorter than flagellar segment 3; galeae shiny or dulled by shagreening; vestiture tawny, ochraceous or white; mostly United States and Canada 85

85(84). Galeae shiny, unshagreened above except at tips; medium-sized bees, about 11 mm. in length; tergum 1 with apical hairs obscuring surface in lateral thirds or slightly less, not medially; vestiture white to extremely pale ochraceous, *bicolorata*, n. sp.

Galeae usually dulled above by shagreening at least in apical halves; small bees, 9 to 11 mm. in length; tergum without plumose apical hairs obscuring surface at extreme sides; vestiture usually ochraceous to yellow ..... *subagilis* Cockerell

86(52). Mesoscutum, scutellum and tegulae without dark hairs; terga 6 and 7 with abundant dark brown hairs; Central America ..... *persimilis* Cockerell

Mesoscutum and scutellum and usually tegulae and vertex of head with at least a few dark brown hairs, *if* dark hairs absent, *then* terga 6 and 7 with hairs all pale as well; United States and Mexico 87

87(86). Tergum 2 with distal pale band not markedly arched or notched along posterior margin, of about same length across tergum and subequal in length to apical area medially; southeastern Mexico ..... *floris* Cockerell

Tergum 2 with distal pale band markedly arched along posterior border so as to be distinctly thinned (rarely interrupted) and shorter than apical area medially; United States and Northern Mexico ..... *montana* Cresson (in part)

FEMALES

1. Mesoscutal and scutellar punctures minute, mesoscutum with large posteromedian area impunctate or with scattered punctures less than ⅓ diameter of mesepisternal punctures; mesoscutal punctures anteromesad of parapsidal lines no larger and mostly smaller than mesepisternal punctures and separated by 2 to 3 puncture widths or more, *expolita*, n. sp.

Mesoscutal and scutellar punctures larger *or* more crowded than described above, or both 2

2 (1). First three sterna with long apicomedian hairs with curled tips; scopal hairs long, curled near tips, with 2 or 3 branches on each side of rachis; first tergum with sparse minute punctures in basal third or less . . *paucipuncta*, n. sp.

First three sterna with apicomedian hairs not so long, not curled near tips; scopal hairs almost always more abundantly branched, with straight tips; first tergum usually with more abundant and larger punctures in basal third to two-thirds 3

3 (2). Thorax with lateral and ventral surfaces, including propodeum, with dark brown or black hairs; terga 2 and 3 with lateral raised areas of interband zones with large, piliferous punctures, surfaces shiny, with no tessellation nor shagreening; supraclypeal area shiny, unshagreened, *hymenoxidis* Cockerell

Thorax with entire lateral surface not usually with dark brown to black hairs, *if* so, *then* terga 2 and 3 with raised lateral areas of interband zones with surfaces at least slightly dulled by shagreening or tessellation or shiny but with extremely fine shagreening; supraclypeal area variously sculptured 4

4 (3). Terga without complete pale pubescent bands, these being reduced to lateral fasciae or absent completely; or, *if* one complete band present, *then* it is band of tergum 2 *and* lower lateral mesepisternal surfaces with dark brown hairs, 5

Terga with complete pale pubescent bands on more than one tergum, *if* complete on only one tergum, *either* not on tergum 1, *or* lower lateral mesepisternal surfaces without dark hairs 12

5 (4). Scopal hairs fuscous or almost entirely so 6

Scopal hairs pale or mostly pale (those of basitarsi often mostly or entirely dark brown) 8

6 (5). Thorax above, including dorsal and posterior faces of propodeum and often upper parts of mesepisterna, pale ochraceous to slightly ferrugineous (fox-red), laterally and ventrally dark brown to black; medium-sized bee, 11 to 13 mm. in length ..... *bicolorata*, n. sp.

Thorax mostly dark brown to black, occasionally with paler hairs peripherally on scutellum, near bases of tegulae and

on dorsum of propodeum; small bees, 9 to 12 mm. in length 7

7 (6). Wing membranes deeply infumate, dark brown; clypeus with surface dulled by coarse reticular shagreening; Cuba, *pullata* Cresson

Wing membranes only slightly infumate near tips; clypeus shiny, at most with delicate shagreening; Oregon, *pullatella*, n. sp.

8 (5). Tergum 1 with punctures of anterior half large, rounded, mostly separated by about ½ a puncture width, surface only delicately shagreened, shiny ..... *dentiventris* Smith

Tergum 1 with punctures of anterior half smaller, usually separated by much more than half a puncture width and often by more than one puncture width, or irregular, surface dulled by dense reticulotransverse shagreening which often obscures punctures 9

9 (8). Terga 2-4 with apical areas shiny, impunctate, without hairs, slightly translucent, reddish brown in color; clypeus not at all protruding ..... *rustica* (Say) (in part)

Terga 2-4 with apical areas moderately dulled by coarse shagreening, *or* with short, appressed or subappressed hairs, *or* punctate, *or* all of these; clypeus occasionally protruding by almost ½ width of eye in profile 10

10 (9). Mesoscutum with surface distinctly shagreened (reticularly); small bees, 10-12 mm. in length; thorax with dorsum with most hairs ferrugineous (more rarely ochraceous) 11

Mesoscutum with surface unshagreened; shiny; medium-sized bees, 11-14 mm. in length; thorax with dorsal hairs mostly pale ochraceous, never ferrugineous, *bimatris*, n. sp. (in part)

11(10). Galeae shiny, unshagreened except at tips.. *bidentis* Cockerell

Galeae dulled by dense shagreening, *trinodis* Robertson (in part)

12 (4). Flagellar segment 2 slightly but distinctly longer than wide; hairs of inner surfaces hind basitarsi brown or dark brown, 13

Flagellar segment 2 as wide as long or wider and/or hairs of inner surfaces hind basitarsi yellow to dark red 18

13(12). Terga 2 and 3 with apical areas with abundant, suberect, dark brown to black hairs; pygidial plate acutely V-shaped, 14

Terga 2 and 3 with apical areas apubescent or with white or ochraceous, suberect hairs; pygidial plate V-shaped, but apex rounded, not acute 15

14(13). Galeae dulled by dense tessellation ..... *micheneri*, n. sp.

Galeae shiny, not tessellate, unshagreened or at most only lightly so ..... *exilis*, n. sp.

15(13). Mesoscutum without dark hairs (or extremely few) and often none on scutellum; forewing and tegulae measures 11 mm. or more in length 16

Mesoscutum with large patch of dark brown hairs, scutellum also with dark hairs; forewing plus tegula measures less than 11 mm. in length 17

16(15). Terga 6 and 7 with lateral tufts of pale ochraceous to white hairs; mesepisterna without dark hairs . . . *menuachus* Cresson

Terga 6 and 7 without lateral tufts of pale hairs; mesepisterna with lower-lateral parts with dark brown to black hairs, *semilupina* Cockerell

17(15). Posterior pronotal lobes with black hairs mixed with the pale; mesoscutal dark hair patch reaching tegulae laterally or almost so; clypeal punctures large, round, separated by about half a puncture width, surface shiny, unshagreened or only slightly so . . . . . *perpolita*, n. sp.

Posterior pronotal lobes without black hairs; mesoscutum without large brown patch posteromedially; clypeal punctures small and crowded, surface dulled by dense reticular shagreening . . . . . *cerussata*, n. sp.

18(12). Scopal hairs with branches gently deflected outward from rachis and hooked downward toward tips so as to appear somewhat S-shaped (especially on upper half of basitarsi and medially on tibiae), branches short, abundant; terga 2 and 3 with apical areas broad, impunctate and apubescent; inner surfaces hind basitarsi with hairs dark brown to black 19

Scopal hairs with straight branches originating in a sharp angle to rachis, or *if* somewhat S-shaped, *then either* terga 2 and 3 with apical areas punctate or pubescent *or* with inner surfaces hind basitarsi with yellow to red hairs, 20

19(18). Posterior lobes of pronotum almost always with black hairs (at least one present); outer surfaces middle basitarsi with hairs dark brown; small bees, hamuli usually with 11-12 hooks, rarely 13 . . . . . *denticulata* Smith

Posterior lobes pronotum usually without black hairs; outer surfaces middle basitarsi with hairs cinereous to pale brown, never dark; medium-sized bees, hamuli usually with 13-15 hooks . . . . . *vernoniae* Robertson

20(18). Tergum 1 with apical area broadly hyaline, colorless; inner surfaces hind basitarsi with hairs dark brown or black; clypeus with shiny median boss; vestiture ochraceous to white . . . . . *tristis* Cockerell

Tergum 1 with apical margin usually opaque, *if* hyaline, only narrowly so *or* inner surfaces hind basitarsi with hairs yellow to red, *or* clypeus without shiny median boss; vestiture variously colored 21

21(20). Tergum 3 with apical area with (a) dark hairs across entire tergum or at least across median third or more, *or* (b) with pale hairs which do not completely obscure surface and which differ from hairs of distal pale band by being less plumose and more erect, *or* (c) with no hairs or punctures and apical apubescent area longer than distal pale band of tergum 2 at least medially 22

Tergum 3 with apical area covered by distal pubescent band which is apical, *if* with apical area not covered by distal

pale band, *then either* (a) apical area apubescent, impunctate, and shorter across tergum than distal pale band of tergum 2, *or* (b) apubescent, impunctate *and* broadly triangular in shape but no wider than ⅓ width of tergum (distal pubescent band reaching margin of tergum in lateral thirds) 55

22(21). Mesoscutum without patch of dark brown to black hairs posteromedially, or few if any present; clypeus often protrudes slightly, in profile by as much as ½ width of eye... 23

Mesoscutum with distinct patch of dark brown to black hairs posteromedially; clypeus rarely protruding by as much as ½ width of eye in profile..... 30

23(22). Tergum 1 with impunctate apical area equal to more than half of basal punctate area medially; tergum 3 often without dark hairs in apical area..... 24

Tergum 1 with impunctate apical area equal to half or less of basal punctate area medially; tergum 3 with apical area often with suberect dark hairs..... 27

24(23). Thoracic hairs white; metasomal pubescent bands white; terga 2 and 3 with apical areas with suberect hairs simple, white or brown..... *snowii* Cresson

Thoracic hairs pale to bright ferrugineous or ochraceous; metasomal pubescent bands usually yellowish; terga 2 and 3 with apical area hairs golden or brown, often with short distinct barbs..... 25

25(24). Veins of hind and fore wings dark brown to black; metasomal sternal hairs mostly dark brown to black; tergum 4 with pale apical band notched medially with area of dark brown to black hairs; terga 2 and 3 with apical areas with dark suberect hairs..... *trinodis* Robertson (in part)

Veins of hind and fore wings mostly red; metasomal sternal hairs mostly ferrugineous or paler, occasionally dark brown; terga 2, 3 and 4 with apical areas with no suberect hairs or these pale in color..... 26

26(25). Galeae shiny above, unshagreened except at tips; terga 2 and 3 with apical areas with suberect hairs long (of about same length as those of distal pubescent band) and abundant (obscuring surface, especially on tergum 3), *perlusa* Cockerell

Galeae dulled above by dense shagreening; terga 2 and 3 with apical areas with suberect hairs shorter and less abundant, scarcely obscuring surfaces ..... *agilis* Cresson

27(23). Terga 2 and 3 with apical areas impunctate and without suberect hairs ..... *ochraea*, n. sp.

Terga 2 and 3 with apical areas punctate and/or with suberect hairs 28

28(27). Terga 2 and 3 with apical areas with suberect, long, pale hairs; flagella usually entirely dark brown to black, *bimatris*, n. sp. (in part)

Terga 2 and 3 with apical areas with dark brown, suberect hairs; flagella usually red below..... 29

29(28). Terga 2 and 3 with apical areas with suberect hairs arising from small but distinct punctures; galeae usually dulled by shagreening ..... *hurdi*, n. sp.

Terga 2 and 3 with apical areas with suberect hairs not arising from distinct punctures; galeae usually shiny, unshagreened except at tips ..... *submenuacha* Cockerell

30(22). Galeae dulled by dense regular tessellation, with long hairs some of which are bent or hooked near tips; terga 2 and 3 with apical areas with abundant, long dark brown to black, suberect hairs arising from minute but distinct punctures; vertex of head and tegulae with abundant dark brown hairs ..... *moorei* Cockerell

Galeal sculpturing various, without hooked hairs, or, *if* tessellate and with hooked hairs, *then* terga 2 and 3 with apical areas impunctate or without dark hairs or both; vertex and tegulae often without dark hairs 31

31(30). Pygidial plate acutely V-shaped; medial tibial scopal hairs reddish brown, anterior and posterior hairs golden yellow; terga 2 and 3 with apical areas with subappressed, dark brown hairs; tegulae testaceous ..... *crocina*, n. sp.

Pygidial plate V-shaped or U-shaped, *if* V-shaped not acutely so, but apex rounded; medial tibial scopal hairs as pale as other scopal hairs; terga 2 and 3 with apical areas various; tegulae usually piceous 32

32(31). Small bees, forewing plus tegula measures about 8 mm. in length; vertex of head and tegulae without dark hairs; thoracic pale hairs white or very pale ochraceous; posterior pronotal lobes never with dark hairs. *humilior* Cockerell

Usually larger bees, *if* forewing and tegula measures 8 mm. or less in length, *then* vertex of head and tegulae with dark hairs, *or* pale hairs of thorax ferrugineous, *or* posterior pronotal lobes with at least a few dark hairs 33

33(32). Small bees, forewing plus tegula less than 8 mm. in length; tergum 2 with distal pale band broadly interrupted medially, forming two lateral oblique fasciae tapering mesally and anteriorly, each fascia about as long as distance between their tips, apical area long, glabrous, *fasciatella*, n. sp.

Usually larger bees, *if* forewing and tegula measures 8 mm. or less, *then* tergum 2 with distal pale band not broadly interrupted medially, apical area often with hairs 34

34(33). Tergum 3 with apical area with abundant simple white hairs arising from small but distinct punctures (hairs may be cinereous or even pale brown medially); tergum 2 with apical area similar but less distinctly punctate; metasomal pale hairs and scopal hairs white; posterior pronotal lobes never with dark hairs ..... *nivea* Robertson

Tergum 3 with apical area usually with abundant dark brown hairs, *if* with simple white hairs, *then* these not arising from distinct punctures; metasomal pale hairs and scopal

hairs often ochraceous to yellow; posterior pronotal lobes often with dark hairs 35

35(34). Terga 2 and 3 with apical areas long (usually medial length greater than medial length of pale band of tergum 3), apubescent, and impunctate, surface dulled by fine, dense, reticular shagreening, as dull as interband zone of tergum 2 (a few scattered, dark brown, short, appressed hairs may be present but, if so, separated by more than length of one of hairs) 36

Terga 2 and 3 with apical areas *either* (a) short (less than length of distal pale band tergum 3), *or* (b) with abundant hairs, pale or dark, *or* (c) punctate, *or* (d) shiny and distinctly less dulled by shagreening than interband zone of tergum 2, *or* some combination of these 38

36(35). Tergum 4 with pubescence along apical margin dark brown to black, without apicomedian apubescent area, *wheeleri* Cockerell

Tergum 4 with apicomedian apubescent triangular area, often with a few dark brown hairs along apical margin or in virtually apubescent area 37

37(36). Tergum 4 with apical apubescent area with abundant, minute punctures obscured by dense tessellation; tergum 2 with interband zone with distinct punctures; mesepisterna usually dulled by fine irregular shagreening, *illata* Lovell and Cockerell

Tergum 4 with apical apubescent area impunctate, surface dulled by dense shagreening as in terga 2 and 3, tergum 2 with interband zone virtually impunctate; mesepisterna with surfaces usually shiny, unshagreened ... *subillata,* n. sp.

38(35). Tergum 2 with apical area impunctate and without hairs (a very few short dark appressed hairs may be present near distal pale band), shiny, extremely finely reticulotransversely shagreened; tergum 2 with interband zone with surface dulled by dense reticular shagreening contrasting with shiny apical area; vertex of head and tegulae with abundant dark brown to black hairs 39

Tergum 2 with apical area either punctate or with abundant appressed to suberect, pale to dark hairs, often dulled by shagreening, *if* glabrous, shiny and impunctate, *then* tergum 2 with interband zone with surface also shiny, not contrasting with apical area; vertex of head and/or tegulae often without dark hairs 40

39(38). Tergum 3 with distal pubescent band usually reaching apical margin at extreme sides; pale mesoscutal hairs anterior to dark patch white to pale ochraceous; scopal hairs ochraceous; tergum 1 with punctures small, separated by about half a puncture width but distinct, surface reticularly shagreened ..... *pallidisignata* Cockerell (in part)

Tergum 3 with distal pubescent band well-separated from apical margin across entire tergum; pale mesoscutal hairs

anterior to dark patch often ferrugineous; scopal hairs usually golden yellow; tergum 1 with basal area punctures large, extremely shallow, crowded, obscured by dense, reticular shagreening ..... *rustica* (Say)

40(38). Tergum 2 with interband zone with distinct, round, regular punctures across entire tergum, may be sparser medially than laterally 41

Tergum 2 with interband zone impunctate or punctures indistinct or irregular in shape and size, or restricted to lateral raised areas 50

41(40). Tergum 3 and often tergum 2 with apical area distinctly punctate, punctures at least slightly greater in diameter than hairs arising from them 42

Terga 2 and 3 with apical areas impunctate or with minute punctures scarcely greater in diameter than hairs arising from them 47

42(41). Small bees, forewing plus tegula equals 8 mm. or less, dorsal thoracic hairs (especially pale hairs) blunt, branches extremely short and abundant making hairs appear thick and clipped; clypeus flat, shiny, punctures coarse, shagreening sparse, delicate and irregular, *paulula*, n. sp.

Small to large bees, *if* forewing plus tegula 8 mm. or less, *then* dorsal thoracic hairs with longer, sparser branches thus appearing thinner and sharply pointed; clypeus often slightly bowed outwards, punctures variable, surface often dulled by reticular shagreening 43

43(42). Tergum 1 with basal area punctures large and deep, medially as large or larger than scutellar punctures but not as deep, well-separated and not obscured by shagreening 44

Tergum 1 with basal area punctures small and shallow, medially distinctly smaller than scutellar punctures, crowded and often obscured by dense shagreening 45

44(43). Posterior lobes of pronotum usually with at least one long black hair mixed with the pale; galeae dulled by tessellation ..... *boltoniae* Robertson

Posterior lobes of pronotum never with black hairs; galeae with at least basal half shiny and not tessellate or shagreened, apical half or less often dulled by fine reticular shagreening ..... *fumosa*, n. sp.

45(43). Galeae shiny, unshagreened above except near tips; tergum 2 with interband zone punctures small, in median third separated mostly by 2 to 3 puncture widths, laterally by 1 to 2 puncture widths, tergum 4 fringed with black hairs ..... *pilleata*, n. sp.

Galeae dulled above by fine reticular shagreening at least in apical third to one-half; tergum 2 with interband zone punctures slightly larger, in median third separated mostly by 1 to 2 puncture widths and laterally by 1 puncture

width or less; tergum 4 with or without fringe of black hairs 46

46(45). Terga 5 and 6 with small lateral tufts of white hairs; mesoscutal dark patch twice as large as scutellar dark patch or almost so (sometimes larger); mesoscutum with pale hairs white to pale ochraceous ..... *tincta*, n. sp.

Terga 5 and 6 without lateral pale hair tufts; mesoscutal dark hair patch equals scutellar dark patch or only slightly larger; mesoscutal pale hairs ochraceous to dull ferruginous ..... *manipularis* Smith

47(41). Clypeus with large crowded punctures, surface shiny, unshagreened; tergum 2 with interband zone punctures regular in size and spacing, not sparser medially; scopal hairs white ..... *pexa*, n. sp.

Clypeus with punctures often small, surface usually somewhat dulled by shagreening, *if* surface shiny and unshagreened, *then* tergum 2 with punctures of interband zone somewhat sparser medially than laterally; scopal hairs often pale ochraceous 48

48(47). Galeae shagreened in apical half or more; tergum 2 with interband zone punctures not markedly sparser medially than laterally, with distal pubescent band usually not interrupted medially ..... *elegans*, n. sp.

Galeae shiny, unshagreened except at tips; tergum 2 with interband zone punctures somewhat sparser medially than laterally, with distal pale band often narrowly interrupted medially 49

49(48). Wing membranes somewhat infumate, yellowish brown; inner surfaces hind basitarsi with hairs orange to dark red ..... *montana* Cresson

Wing membranes clear, not infumate; inner surfaces hind basitarsi with hairs dark reddish brown to black, *coreopsis* Robertson

50(40). Galeae dulled by dense, coarse shagreening or tessellation, *robustior* Cockerell

Galeae shiny, unshagreened except at tips or only extremely delicately so 51

51(50). Tergum 3 and usually 2 with apical area with hairs white to brown, long and silky, suberect, often curved away from surface; pale body hairs and scopal hairs white; clypeal punctures small, surface dulled by dense reticular shagreening ..... *gelida*, n. sp.

Terga 2 and 3 with apical area hairs dark brown to black, short, subappressed, straight, not silky but appearing rigid; pale mesoscutum and often scopal hairs ochraceous to pale ochraceous 52

52(51). Small bees, wing plus tegula measures 8 mm. or less in length; tergum 3 with apical area less than half length of distal pale band medially, with short subappressed brown hairs arising from minute punctures ..... *limbus*, n. sp.

Larger bees, *if* wing plus tegula measures 8 mm. or less, *then* tergum 3 with apical area at least half as long as distal pale band medially *or* provided with subappressed black hairs but not punctate at all 53

53(52). Terga 5 and 6 without lateral tufts of pale hairs; mesepisterna and clypeus often with lower parts with dark brown to black hairs; flagellum often dark brown to black below ..... *confusa* Cresson

Tergum 5 and usually tergum 6 with lateral tufts of pale hairs; mesepisterna and clypeus usually without dark hairs; flagellum usually red below 54

54(53). Tergum 2 with distal pale band distinctly and abruptly interrupted medially (lateral fasciae not tapered to midline); mesepisterna without dark hairs below; inner surfaces hind basitarsi with hairs orange to red, *interrupta,* n. sp.

Tergum 2 with distal pale band not interrupted medially, *or* if so, *then* lateral fasciae tapered to midline; mesepisterna often with dark brown hairs below, inner surfaces hind basitarsi with hairs dark reddish brown to black, *persimilis* Cockerell

55(21). Terga 2-4 with apical areas translucent, colorless to pale yellowish brown; inner surfaces hind basitarsi with hairs yellow to red 56

Terga 2-4 with apical areas piceous, *if* somewhat translucent, *not* pale yellowish brown but dark brown and opaque; inner surfaces hind basitarsi with hairs often dark brown to black 58

56(55). Mesoscutum with no or few dark brown hairs; terga 2 and 3 with apical areas with hairs white; terga 5 and 6 with hairs white to ochraceous ..... *saponellus* Cockerell

Mesoscutum with large patch of brown hairs; terga 2 and often 3 with apical area hairs dark brown; terga 5 and 6 often with dark brown hairs 57

57(56). Wing membranes somewhat infumate; terga 3-5 with basal areas (*e. g.* usually telescoped under preceding segment) with white hairs; clypeus somewhat bowed outwards, *velutina* (Cockerell)

Wing membranes colorless, clear; terga 3-5 with basal area hairs brown; clypeus relatively flat ..... *vernalis,* n. sp.

58(55). Small bees, forewing plus tegula measures 7.0 to 8.5 mm. in length; pygidial plate acutely V-shaped; flagellum dark reddish brown to black except small dark red ventral spot on segments 3 to 10; tergum 2 with distal pubescent band narrowly interrupted medially; inner surfaces hind basitarsi with dark hairs ..... *microsticta* Cockerell

Small to medium-sized bees; *if* forewing plus tegula measures 8.5 mm. or less, *then* pygidial plate not acutely V-shaped but with apex rounded, and/or flagellum dark red below; tergum 2 often with distal pale band uninter-

rupted; inner surfaces hind basitarsi often with yellow to red hairs 59

59(58). Tergum 2 with interband zone impunctate or virtually so, with dark hairs suberect to erect; inner surfaces hind basitarsi with dark reddish brown to black hairs, *grindeliae* Cockerell

Tergum 2 with interband zone with distinct punctures, *if* almost impunctate, *then* with hairs pale and/or appressed to subappressed; inner surfaces hind basitarsi often with hairs yellow to red 60

60(59). Pygidial plate acutely V-shaped; mesoscutum with posteromedian area with punctures round, deep, crowded, separated mostly by half a puncture width . . . *relucens*, n. sp.

Pygidial plate V-shaped but with rounded apex (sometimes worn to acute point), *if* acute, *then* posteromedian area mesoscutum impunctate or with punctures separated mostly by one puncture width or more 61

61(60). Small bees, forewing plus tegula less than 8 mm. in length; inner surfaces hind basitarsi with hairs yellow to red; galeae dulled by dense tessellation, with long hairs some of which are hooked or bent near tips *melanura* (Cockerell)

Larger bees, *if* forewing plus tegula measures less than 8 mm. in length, *then either* inner surfaces hind basitarsi with hairs dark brown *and/or* galeae shiny, not tessellate; galeal hairs often short and never hooked near tips 62

62(61). Medium-sized bees, forewing plus tegula measures 9 to 10 mm. in length; tergum 2 with interband zone with lateral raised areas with distinct punctures of two sizes, one large and seemingly directed somewhat posteriorly, the other minute; inner surfaces hind basitarsi with hairs dark brown ..... *pallidisignata* Cockerell (in part)

Smaller bees, *if* forewing plus tegula equals 9 mm. or more in length, *then* tergum 2 with interband zone impunctate or punctures all of same size, *or* inner surfaces hind basitarsi with hairs yellow to red 63

63(62). Medium-sized bees, forewing plus tegula measures more than 8 mm. in length; inner surfaces hind basitarsi with hairs yellow to red; tergum 2 with distal pale band extremely narrowly interrupted medially; mesoscutal dark hair patch about equal to scutellar dark patch in size, *rufipes*, n. sp.

Smaller bees, *if* forewing plus tegula measures more than 8 mm. in length, *then either* inner surfaces hind basitarsi with hairs dark, *or* tergum 2 with distal pubescent band uninterrupted *or* mesoscutal dark hair patch smaller than scutellar dark patch, *or* some combination of these 64

64(63). Galeae dulled above by dense reticular shagreening; inner surfaces hind basitarsi with hairs usually yellow to red, rarely dark reddish brown; pale vestiture ochraceous to yellow (especially on mesoscutum); mesoscutum usually

without dark hairs or dark patch smaller than scutellar dark patch ..... *subagilis* Cockerell

Galeae shiny, not dulled above by dense shagreening except near tips (less than apical half), *if* dulled by shagreening, *then* either inner surfaces hind basitarsi with dark hairs, *or* pale vestiture white, *or* mesoscutum with large dark hair patch (at least as large as scutellar dark patch) .. 65

65(64). Tergum 2 with interband zone with appressed to subappressed, white pubescence, dark spinelike hairs absent, with distal pale band composed of relatively long, overlapping plumose hairs, not interrupted medially unless worn .. 66

Tergum 2 with interband zone with appressed to subappressed, dark brown to black, spinelike hairs, *or if* dark hairs absent, *then* distal pale band medially composed of short, scalelike, discrete (not overlapping except near base of pale band) hairs, often extremely narrowly interrupted medially 68

66(65). Galeae dulled above by shagreening at least in apical third to one-half; mesoscutum usually with dark hairs posteromedially ..... *utahensis*, n. sp.

Galeae unshagreened except near tips; mesoscutum without dark hairs 67

67(66). Tergum 2 with apical area apubescent, shiny, subequal to distal pale band in length medially or longer than half length of distal pale band, interband zone with distinct punctures about equal in diameter to punctures of basal area and separated mostly by half to one puncture width, *brevipyga*, n. sp.

Tergum 2 with apical area obliterated by distal pale band, or, *if* apubescent, shorter than half length of distal pale band medially, with interband zone with minute punctures distinctly smaller than those of basal area and separated mostly by one or more puncture widths, *verbesinarum* Cockerell

68(65). Tegulae with abundant dark brown hairs; tergum 1 with apical area with abundant, short, closely appressed, dark brown hairs ..... *personatella* Cockerell

Tegulae with hairs white to ochraceous; tergum 1 with apical area apubescent or with appressed hairs white (a few dark brown appressed hairs sometimes present anterolaterally) 69

69(68). Terga 2 and 3 with distal pubescent bands at least near midline composed of short, scalelike, appressed, plumose hairs which scarcely overlap laterally or do not; tergum 2 with interband zone punctures regular in size and spacing (often slightly sparser medially) ..... *appressa*, n. sp.

Terga 2 and 3 with distal pale bands composed of relatively long plumose hairs overlapping laterally, not seemingly scalelike; tergum 2 often with punctures irregular in size and spacing 70

70(69). Mesoscutum with posteromedian area with punctures separated mostly by less than two puncture widths, *monoensis*, n. sp.

Mesoscutum with posteromedian area punctures separated mostly by more than two puncture widths . . . . *lutulenta*, n. sp.

Melissodes (Eumelissodes) agilis Cresson

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Melissodes agilis is without doubt the most common species of the genus *Melissodes* in North America. The females are distinctive in the usually red thoracic hairs (without posteromedian brown patch), the red to reddish brown wing veins, the dulled galeae and

the ochraceous scopal hairs. The males can be recognized by the hyaline tergal margins, the dulled galeae, the yellow maculae on the mandibles and labrum and the entirely yellow clypeus, the yellow to pale red wing veins, the ochraceous to red thoracic hairs and the short first flagellar segment. Both sexes closely resemble certain other species of the subgenus *Eumelissodes* in one or more of these characteristics. These are discussed in the diagnosis of the species whose descriptions follow that of *agilis*.

Female. Measurements and ratios: N, 20; length, 10-13 mm.; width 3.5-4.5 mm.; wing length, M = 3.46 ± 0.159 mm.; hooks in hamulus, M = 13.45 ± 0.223; flagellar segment 1/segment 2, M = 1.81 ± 0.027.

Structure and color: Integument black except as follows: apical half of mandible, lower surface of flagellar segments 3-10 (and often apex of segment 2), and distitarsi rufescent; eyes gray to bluish gray, rarely greenish or black with violet reflections; wing membranes hyaline, colorless, veins red to reddish brown, pterostigma yellow to red; tibial spurs yellow to red.

Clypeus with small round regular punctures separated by half to one puncture width, surface dulled by coarse regular reticular shagreening, often with short median longitudinal carina in apical half, clypeus slightly protruding beyond eyes in profile but by no more than half width of eye; supraclypeal area sculptured as clypeus but often impunctate medially; galeae dulled above by dense, fine tessellation; maxillary palpal segments in ratio of about 4.5:3.5:3.3:1.0; vertex with flattened lateral areas with small round punctures separated mostly by one to three puncture widths, surface dulled by irregular reticular shagreening. Mesoscutum with deep round punctures separated by half to one puncture width, slightly larger and sparser in posteromedian area, surface shiny, sparsely or not at all shagreened; scutellar punctures similar to mesoscutal but slightly more crowded; metanotum with punctures half diameter of scutellar, separated mostly by half to one puncture width, surface dulled by extremely fine, reticular shagreening; propodeum with dorsal surface reticulorugose, coarsely so basally, posterior surface with coarse punctures except upper triangle, lateral surfaces similar to posterior but punctures more crowded, surfaces dulled by dense regular tessellation; mesepisternum with lateral surface with large shallow punctures separated mostly by half a puncture width or less, surface shiny, unshagreened or finely so. Metasomal tergum 1 with basal three-fifths or slightly less punctate (to apex at extreme

sides), punctures round, shallow, separated mostly by one to two puncture widths, surface dulled by fine tessellation, apical area impunctate with surface shiny, extremely finely reticulotransversely shagreened; tergum 2 with basal zone with minute round punctures separated mostly by half to one puncture width, surface shiny but with fine reticular shagreening, interband zone with small irregular punctures separated by one to three puncture widths, sparser medially than in lateral raised areas, surface dulled by reticulotransverse shagreening, apical area impunctate or with minute punctures no broader than base of hairs arising from them, separated by two to four puncture widths, surface moderately shiny, with fine reticulotransverse shagreening; terga 3 and 4 similar to tergum 2 but punctures of interband zone somewhat more distinct and more abundant and apical zone smaller or absent; pygidial plate broadly V-shaped with rounded apex.

Hair: On face and genal areas pale ochraceous to yellow, on vertex yellow to bright rufescent, vertex with or without brown hairs (never abundant). Thorax with sides pale ochraceous to pale rufescent, above ochraceous to bright rufescent. Metasomal tergum 1 with long basal and lateral hairs ochraceous to yellow or slightly rufescent, apical area glabrous or with sparse, minute, appressed, brown to yellow hairs basally and laterally; tergum 2 with basal pubescence long, white to yellow, interband zone with short; appressed to subappressed, white to pale brown, relatively simple hairs, distal pale band yellow to white, broad laterally (but usually not reaching apical margin) to narrow medially, usually narrowly interrupted medially, apical area with relatively simple, appressed to subappressed, white to yellow hairs obscuring but not completely hiding surface; tergum 3 similar to 2 but basal tomentum dark brown, interband zone hairs dark brown, distal pale band not interrupted, apical area shorter; tergum 4 similar to 3 but distal pale band reaches apex across entire tergum, occasionally with minute apicomedial area of brown hairs; terga 5 and 6 dark brown except white to yellow tufts at extreme sides; sterna yellow to reddish brown medially and paler at extreme sides. Legs pale (white to yellow) except as follows: fore tarsi, often middle basitarsi on outer surfaces, fore and middle tibiae on outer surfaces near apices, hind basitarsi on outer surface at apices, and usually on and surrounding basitibial plates brown; inner surfaces of hind basitarsi with red to reddish brown hairs; scopal hairs ochraceous to yellow.

Male. Measurements and ratios: N, 20; length 9-12 mm.; width, 3.0-4.0 mm.; wing length, $M = 3.20 \pm 0.217$ mm.; hooks in

hamulus, $M = 11.65 \pm 0.274$; flagellar segment 2/segment 1, $M = 7.37 \pm 0.164$.

Structure and color: Integument black except as follows: clypeus and base of mandible yellow; labrum white or cream-colored with brown apical margin (extremely rarely all brown); eyes green to gray or grayish blue; flagellum yellow to red below, dark red to brown above; tegulae usually testaceous, occasionally piceous; wing membranes colorless, veins yellow; apical margins of terga hyaline, colorless to yellow (in some eastern specimens translucent brown); distitarsi rufescent; tibial spurs white to yellow.

Clypeus protruding beyond eye in profile by about half width of eye; eyes strongly converging toward mandibles; first flagellar segment with minimum length equal to about one-sixth or one-seventh maximum length of second segment, penultimate segment about three times as long as broad (minimum width, maximum length), flagellar segments without longitudinal lateral depressions; maxillary palpal segments in ratio of about 4:3:3:1. Sculpturing as in female except as follows: clypeus with surface often moderately shiny; mesepisternum with surface often somewhat dulled by fine, irregular shagreening; metasomal tergum 1 medially with basal four-fifths to five-sixths with small punctures separated by one to three puncture widths; interband zone of terga 2 and 3 with slightly more abundant and larger punctures, surface moderately shiny, with reticular shagreening; hyaline apical areas of terga 1 to 5 shiny or moderately so, reticulotransverse shagreening extremely fine; sterna with surfaces shiny to moderately so, usually with distinct regular reticular shagreening.

Sternum 7 with median plate subtriangular in shape; larger than lateral plate in area, with abundant short hairs ventrally; lateral plate subtriangular; membranous area between plates almost half size of lateral plate in area, narrow; apicomedial margin between median plates with strong curved carinae on each side. Sternum 8 broad near apex; strongly emarginate apicomedially; with ventral tubercle entire or slightly bidentate, not reaching apical margin of sternum; with several to many hairs on apical margin. Gonostylus slender, tapering apically, not distinctly capitate, in length equal to more than half length of gonocoxite, with abundant short hairs laterally on basal half; spatha about three times as broad as long; gonocoxite with spicules of upper inner surface all or mostly pointed or hairlike; penis valve with prominent dorsolateral lamella which ends proximally in an inflected tooth near spatha (Figs. 72-75).

Hair: Color of vestiture as in female except as follows: generally more males appear pale rather than bright rufescent than females; vertex usually without brown; metasomal tergum 1 with basal four-fifths to five-sixths with long pale hairs and these medially at least long enough to reach apical margin although not abundant enough to completely hide apical area; tergum 2 with distal pale band often not interrupted medially, usually as long as or longer than apical area medially, interband zone usually with abundant long pale suberect hairs; terga 3-5 similar to 2 but basal zone tomentum brown, interband zones usually with scattered pale pubescence as well as suberect hairs and distal pale bands progressively closer to apical margin; terga 6 and 7 with long white to ochraceous or yellow hairs; sterna all pale or yellowish medially; legs white or ochraceous except as follows: inner surfaces of basitarsi and usually distitarsi yellow to reddish yellow.

Geographical Variation. *Melissodes agilis* is distributed throughout the United States (except Florida), southern Canada and northern Mexico (Fig. 9). It is remarkably uniform throughout this range; the chief variations being the degree of brightness of the yellow or red vestiture and in size. In neither of these characteristics is there a marked geographical trend. However, male specimens from eastern parts of the range tend to have the apical hyaline margins of the metasomal terga darker in color than specimens from elsewhere in the range. Also, specimens, especially females, from the northern prairie states and from the southcentral and southwestern provinces of Canada tend to have the vestiture paler or duller in color than elsewhere. In neither of these two cases is there an abrupt step in the clines which must exist and it would be difficult, if not impossible, to delimit clear-cut subspecies.

Bionomics. Very little has been published concerning the nesting habits of *Melissodes agilis.* Rau (1922, p. 34) states that *agilis* was found nesting on a baseball diamond on July 24, 1915. A single female had begun a single burrow. No cells or provisions were yet present. The burrow ". . . was five inches deep, and went downward quite precipitously." A second female was observed by Rau on August 22, 1915 at its horizontal burrow in the face of a clay bank. Custer (1928) reports a female which was possibly *M. agilis* using the same burrow entrance as eight females of *Svastra obliqua* (Say) (see LeBerge, 1956, pp. 974, 975).

M. agilis is apparently an oligolege of the composite genus *Helianthus.* Robertson (1926, p. 379) lists this species as oligolectic

on the composite tribes Astereae and Heliantheae. Out of almost 6,000 bees available to the author for study, a total of 2,135 had floral data attached. Out of these 2,135 bees, 1,909 had been taken on some species of the family Compositae and, more specifically, 1,608 had been taken on some species of *Helianthus*. These data are summarized in Table IV. It is evident that *Helianthus* pollen plays an overwhelmingly important role in the nutrition of this species. Of other pollens only the Compositae are of much importance and no single genus (or even tribe) of the Compositae plays nearly as important a role as does *Helianthus*.

Table IV. Summary of Floral Records for *Melissodes agilis*.

Plant Data			Records of *M. agilis*			
Family	Number of genera	Approximate number of species	Number of collections	Number of females	Number of males	Total number of bees
Compositae (other than *Helianthus*)	35	43	144	63	255	318
Helianthus spp.	1	15	450	428	1,193	1,621
Leguminosae	5	7	32	13	56	69
Brassicaceae	3	4	21	7	50	57
Verbenaceae	1	1	9	1	43	4
Labiatae	2	2	3	2	11	13
Hydrophyllaceae	2	2	3	2	1	3
Others (12)	15	15	18	4	36	40
Totals	64	89	670	520	1,645	2,165

Type Material. The lectotype male of *agilis* (No. 2315) with two male paratypes from Texas are in the collection of the Philadelphia Academy of Sciences. The lectotype female of *aurigenia* (No. 2332) and allotype male (No. 2332.2) both from Colorado are in the collection of the Philadelphia Academy of Sciences. The paratypes of *aurigenia* also in the Philadelphia Academy of Sciences collection include three females from Colorado, Louisiana and Canada, respectively, and five males from New York, Virginia, Kansas and Utah. Two female paratypes (Nos. 2332.3 and 2332.5) are not of

the same species but should be referred to *Melissodes perlusa* Cockerell which is redescribed below.

Distribution. The United States (except Florida), southern Canada and northern Mexico (Fig. 9). This species has been collected from April until mid-November, but chiefly during the months of July, August and September. In addition to the type specimens, females and males have been examined from the localities listed below (localities reported in the literature are included).

ALABAMA: Decatur; Mobile. ARIZONA: Arlington; Carr Canyon (Huachuca Mts.); Chambers; Douglas (and 8 miles N. E.); Flagstaff (and 4 miles N., 7 miles S. and 8 miles N. E.); Fredonia; Grand Canyon; Hereford; Mayer; Mesa (6 miles E.); Nogales; Oak Creek Canyon; Palmerlea; Payson; Phoenix; Prescott; Rosemont; San Francisco Mts.; Sedona (15 miles N.); Show Low; Sonoita (10 miles E. and 11 miles W.); Thatcher; Tucson (and 10 miles S.); Turner; Willcox; Williams; Yuma. CALIFORNIA: Altadena; Altamont (Mt. House Creek); Anaheim; Antioch; Arvin; Bakersfield; Bear Valley; Bishop; Canby; Carbona; Catalina Island; Chino; Claremont; Clear Lake (Soda Bay); Clovis; Coalinga; Colton; Corona; Corral Hollow; Costa Mesa; Davis; Dos Palos; Downey; East Highlands; Exchequer; Firebaugh; Fresno; Hemet; Hueneme; Huntington Beach; Huntington Park; Indio; Kingsburg; Lake City; Lake Tahoe; Lancaster; Lemoore; Lone Pine; Los Angeles; Los Banos (5 miles S.); Mira Loma; Modesto; Monrovia Canyon; Mountain View; Oakley; Ontario; Onyx; Orange; Oxalis; Palm Springs; Pasadena; Patterson; Pleasanton; Redlands; Redwood City; Reseda; Riverside; Rock Creek; Sacramento; Sacramento Co.; San Bernardino Co.; San Jacinto; San Jose; Shafter; Torrance; Tracy; Turlock; Twain Harte; Vernalis; Visalia; Walnut Creek, Contra Costa Co.; Wasco; Westley; Whittier; Wood Lake, Tulare Co.; Woodland Hills. COLORADO: Antonito; Aurora; Baca Co.; Berkley; Boulder; Brighton; Buckeye; Canfield; Carson Camp; Cimarron; Clear Creek; Colorado Springs; Cortez; Crowley; Denver; Dixon Canyon; Durango; Eads; Elbert; Fort Collins; Fruita; Gilpin (Lump Gulch) Co.; Glen Haven; Glen Park; Glenwood Springs; Golden; Golden (Chimney Gulch); Goodview; Grand Junction; Great Sand Dunes, Alamosa Co.; Greeley; Trinidad; Jim Creek (near Boulder); Jumbo Reservoir; La Junta; Lamar; Leadville; Logan Co.; Longmont; Maxwell City; Meeker; Mesa Verde; Midway (5 miles N.); Mt. Manitou, El Paso Co.; Ovid (3 miles E.); Palisade; Pingree Park; Platte Canyon; Poudre Canyon; Pueblo; Rifle Gap; Rock Creek; Rocky Ford;

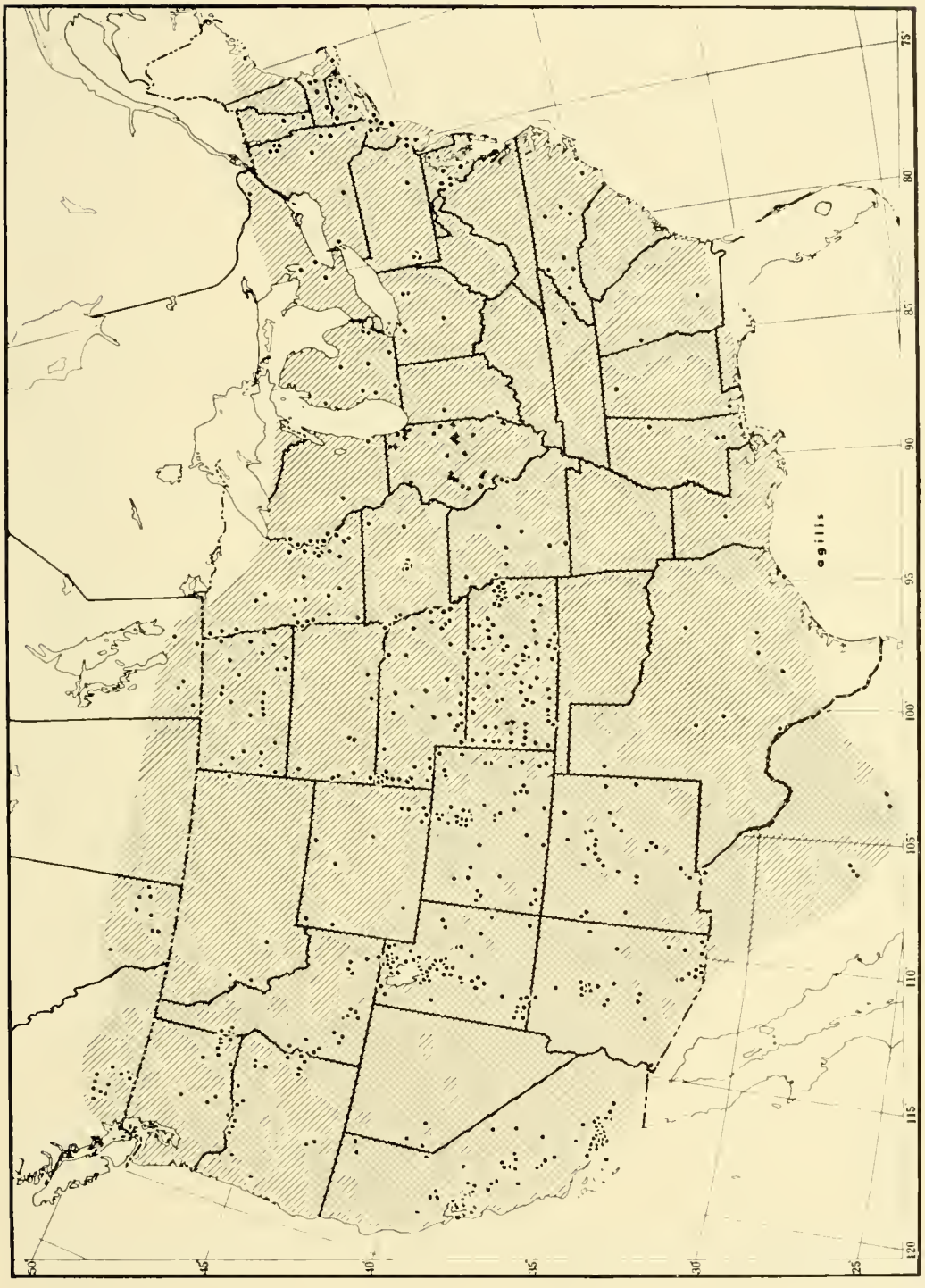


FIG. 9. Map showing the known distribution of *M. (Eumelissodes) agilis* Cresson.

Springfield (3 miles N. in Lone Rock Draw); Sterling; Stratton; Stratton (Landaman Creek); Ten-sheep Ranch; Timpas; Ute Creek (Sage Flats); White Rock (near Boulder); Wray. CONNECTICUT: Colebrook; Storrs; Wallingford; Westville. DISTRICT OF COLUMBIA: Bennings (Eastern Branch); Washington. GEORGIA: Carrollton; Tifton. IDAHO: Aberdeen (and 2 and 6 miles N. E.); Bliss; Brunneau; Buhl; Central Grade, Nez Perce Co.; Coyote Grade, Nez Perce Co.; Downey; Emmett (10 miles E. on Squaw Creek); Fort Hall (near Blackfoot); Franklin; Grandview; Jerome; Lewiston; Midvale (9 miles S. W.); Moscow; Mountain Home; Nampa; Parma; Tuttle; Twin Falls. ILLINOIS: Algonquin; Ashkcum; Bath; Beardstown; Beverly Hills; Bloomington; Carlinville; Champaign Co.; Charleston; Chicago; Cook Co.; Danville; Decatur; Devil's Neck (10 miles N. of Havana); Downers Grove; Edgebrook; Evanston; Fulton (3 miles S.); Havana; Hillview; Macoupin Co.; Manitou; McHenry; Meredosia; Mt. Carmel; Oak Park; Seymour; Urbana; Wellington. INDIANA: LaFayette; Vincennes. IOWA: Ames; Boone (4 miles N. W., 1 mile E. and 5 miles S. E.); Decorah; Ledges State Park; Montpelier; Sergent Bluffs; Sioux City; Vinton. KANSAS: Allen Co.; Anderson Co.; Arkansas City; Assaria; Baldwin; Baldwin Junction; Blue Rapids; Burdett; Butler Co.; Caldwell; Chase (5 miles W.); Cheyenne Co.; Clark Co.; Clay Co.; Cloud Co.; Coldwater; Cullison; Decatur Co.; De Soto; Dickinson Co.; Dodge City; Douglas Co.; Edwards Co.; Garden City; Garnett; Great Bend; Harper Co.; Harvey Co.; Hays; Hodgeman Co.; Hoffee; Hutchinson; Jetmore (10 miles S.); Johnson (2 miles N.); Kendall (3 miles E.); Kingman; Kismet; Lake View, Douglas Co.; Lakin; Larned; Lawrence; Liberal; Logan Co.; Lone Star Lake, Douglas Co.; Manhattan; Marysville; Mayfield; Meade; Meade Co. St. Park; Medora; Neosho Co.; Nickerson; North Topeka; Norton Co.; Olathe; Osborne Co.; Pottawatomie Co.; Reece; Reno; Republic Co.; Richfield (7 miles S.); Riley Co.; Rooks Co.; Russell Co.; Saline Co.; Scott City (8 miles N.); Scott Co.; Sharon Springs; Sherman Co.; Smith Co.; Sunflower; Syracuse; Thomas Co.; Topeka; Tribune (10 miles E.); WaKeeney; Wallace Co.; Wellington; Wichita; Wichita Co.; Wilson Co. LOUISIANA: "La." MAINE: Waldoboro. MARYLAND: Cabin John; Chesapeake Beach; Jessups; Lakeland; Plummers Island. MASSACHUSETTS: Chicopee; Forest Hills; Holden; Lexington; Wellesley; Woods Hole. MICHIGAN: Allegan Co.; Constantine; East Lansing; Grand Rapids; Lewawee Co.; Macomb Co.; Manistee Co.; Midland Co.; Utica. MINNESOTA: Alexandria; Big Stone Co.; Browns Val-

ley; Evan; Faribault; Grant Co.; Hallock; Hastings; Itasca State Park; Lake City; Lake Vadnais, Ramsey Co.; Mallory; Marshall Co.; Mound Springs State Park, Rock Co.; Muskoda; North Branch; Olmstead Co.; Ortonville; Park Rapids; Pine Co.; Powder Plant Woods, Ramsey Co.; Renville; Rochester; Sedan; St. Anthony Park; St. Cloud; St. Paul; Traverse Co.; Washington Co.; Yellow Medicine Co. Mississippi: Camp Shelby (near Hattiesburg); Hattiesburg; West Point. Missouri: Branson; Cameron (10 miles N.); Columbia; Holden; Kansas City; Ozark Lake; Sedalia; Shrewsbury; Springfield; St. Louis. Montana: Fairview; Hamilton; Missoula; Whitehall. Nebraska: Agate; Bennet; Bloomington; Bridgeport; Broken Bow; Cambridge; Cedar Bluffs; Collins; Crawford; Fairmont; Gering; Glen; Gordon; Haigler; Halsey; Hamlet; Hardy; Harrison; Hitchcock Co.; Jim Creek, Sioux Co.; Kearney; Kimball; Lincoln; Lodgepole; Long Pine; Malcolm; Maywood; McCook; Mitchell; Monroe Canyon, Sioux Co.; Nebraska City; Neligh, Niobrara; North Platte; Omaha; Oxford; Palisade; Pine Ridge; Sidney; Sioux Co.; Union; Valentine (Valentine Lakes Refuge); Wabash; Warbonnet Canyon, Sioux Co.; West Point. Nevada: Fallon; Pyramid Lake, Washoe Co.; Reno. New Hampshire: Hanover. New Jersey: Gloucester Co.; Monmouth Beach; Orange; Palmyra; Ramsey; Snake Hill. New Mexico: Albuquerque; Alto; Belen; Capitan; Carrizozo; Cuervo; Fort Wingate; Gallup; Jemez Springs; Las Cruces; Las Vegas; Madrid; Magdalena Mts.; Maxwell; Mesilla; Omega; Organ Mts.; Portales; Rio de los Frijoles; Romeroville; Rowe; Sandia Mts.; San Ignacio; San Jon; Santa Fe (and 12 miles S. E.); Sapello; Socorro; Taos; Vaughn. New York: Albany; Astoria (Long Island); Bronx Park; Brooklyn; Buffalo; Central Park; Elizabethtown; Gloversville; Great Kills (Staten Island); Hope; Ithaca; Keene Valley, Essex Co.; New Baltimore; New Rochelle; New Russia; Orient; Pelham; Wilmington. North Carolina: Aberdeen; Biltmore; Boone; Bostic; Burgaw; Burlington; Newton; Sanford; Smokemont. North Dakota: Bismarck; Clifford; Dickinson; Drake; Edgeley; Fargo; Grafton (4 miles E.); Lakota; Mandan; Marmarth; McKenzie; Medora; Monango; Mott; New Rockford; Oakdale; Oakes; Pleasant Lake; Rugby; Schafer; Sheldon; Steele; Valley City; Washburn; Williston. Ohio: Barberton; Columbus; Summit Co.; Tiffin. Oregon: Arlington; Corvallis; Cove; Echo; Hood River; Huntington; Ione; Juntura (6 and 8 miles E.); La Grande; North Powder; Ontario; Oregon City; Silver Lake; Summer Lake; The Dalles (and 14 miles E.); Vale (Malheur River Canyon). Pennsylvania: Allegheny Co.; Harrisburg; North Braddock; Philadelphia; Pittsburg.

RHODE ISLAND: Kingston; Providence; Scituate. SOUTH DAKOTA: Ardmore; Buffalo (3 miles S.); Cedar Pass (Badlands); Clearfield; Custer; Deadwood (and 10 miles S.); Elk Point; Interior (White River); Jefferson (3 miles S.); Platte. TENNESSEE: Knoxville. TEXAS: Adrian; Austin; Bexar Co.; Colorado City; Dallas; Del Rio; Fedor, Lee Co.; Galveston; San Angelo. UTAH: Avan Canyon; Bear Lake; Bert; Big Cottonwood Canyon (Wasatch Mts. near Fort Bench); Bluff; Bountiful; Cache Junction; Cache Valley; Clover; Collinston; Corinne; Curlew; Delta; Deweyville; Dugway Proving Ground, Tooele Co.; Erda; Eureka; Far West; Ferron; Fillmore; Fort Duchesne; Garfield; Goshen; Grantsville; Green River; Hatton; Helper; Hurricane; Hyrum; Indianola; Jericho; Johnson's Pass, Tooele Co.; Kaibab Forest; Kelton; Lampo; Lake Point; Laketown; Lehi; Lincoln; Logan; Logan Canyon; Magna; Moab; Morgan; Mt. Carmel; Mt. Zion National Forest; Myton; Nephi; Oak City; Ogden; Paragonah; Park Valley; Parowan; Penrose; Petersboro; Pintura; Plain City; Pleasantview; Price; Promontory; Providence; Provo; Richfield; River Heights; Rockville; Roosevelt; Rozelle; Salt Lake City; Saltair; Sevier; Silver City; Skull Valley; Smithfield; Spanish Fork Canyon; Springville; Thistle; Timpie; Tooele; Topaz; Utah Lake; Valley City Junction; Washakie; West Utah Lake; Zion National Park.* VERMONT: Townshend; Woodstock. VIRGINIA: Camp Peary; Falls Church; Four-mile Run (Near mouth of). WASHINGTON: Clarkston; Lind; Maryhill; Penawawa; Pullman, Riparia; Sunnyside; Walla Walla; Wawawai; Wenatchee; Yakima. WISCONSIN: East Farmington; Hudson; Maiden Rock; Milwaukee; Prescott; Randall, Burnett Co.; Warrens; Yellow River (mouth of), Burnett Co. WYOMING: Casper; Cheyenne; Clifton; Diamond Ranch, Platte Co.; Flat Creek; Grand Teton National Park; Granite Canyon, Laramie Co.; Green River; Laramie (28 miles E.); Sheridan; Wheatland (N. Fork of Green River); Worland; Yellowstone National Park. *Canada.* ALBERTA: Calgary; Lethbridge; Medicine Hat; Morrin; Scandia; Suffield; Taber (Oldman River); Welling; Whitla. BRITISH COLUMBIA: Ashcroft Manor (3 miles W.); Fairview; Kamloops; Keremeos; Lillooet; Nicola; Okanagan Falls; Oliver; Spencers Bridge (15 miles E.); Summerland; Thompson River; Vernon; Walhackin. MANITOBA: Altona; Aweme; Brandon; Lauder; Treesbank. NORTHWEST TERRITORY: "N. W. T." (mislabeled or misinterpreted?). ONTARIO: Guelph; Ottawa; Stroud; Toronto. *México.* CHIHUAHUA: Allende; Jiménez (10 and 17 miles W.); Ciudad Juarez; Salaíces. COAHUILA: San Pedro de Colonias. DURANGO: Torreón.

Flower Records. In this list are included flower records reported in the literature. *Abutilon theophrasti, Althaea rosea, Aplopappus spinulosus, Arctium* sp., *Argemone* sp., *A. platyceras, Bidens aristosa, B. laevis, Blephilia hirsuta, Brassica juncea, Braunerla pallida, Carduus crispus, Carya pecan, Cassia* sp., *C. chamaecrista, C. fasciculata, Centromadia pungens, Chrysopsis hispidus, Chrysothamnus* sp., *Cirsium* sp., *C. altissimum, C. discolor, C. lanceolatum, C. undulatum, Clematis* sp., *Cleome* sp., *C. lutea, C. serrulata, Convolvulus* sp., *Coreopsis* sp., *C. lanceolata, C. palmata, C. tripteris, Cosmos* sp., *Datura metaloides, Enceliopsis* sp., *Engelmannia pinnatifida, Ericameria palmeri, Eupatorium* sp., *E. purpureum, Eustoma artemifolium, Gaillardia* sp., *G. cristata, Gilia sp., Grindelia* sp., *G. squarrosa, Gutierrezia* sp., *G. sarothrae, Haplopappus* sp., *Helenium autumnale, H. laciniatum, Helianthus* sp., *H. annuus, H. atrorubens, H. bolanderi, H. ciliaris, H. coronarius, H. divaricatus, H. grosse-serratus, H. laetiflorus, H. lenticularis, H. maximillianus, H. mollis, H. petiolaris, H. pumulis, H. radulus, H. rigidus, H. salicifolius, H. scaberrimus, H. subrhomboideus, H. tuberosus, Heliopsis* sp., *Heliotropium* sp., *Hibiscus* sp., *Ipomoea* sp., *Lactuca pulchella, Lepachys pinnata, Liatris pycnostachya, Medicago sativa, Melilotus* sp., *M. alba, Mentha canadensis, Monarda fistulosa, Penstemon* sp., *Pepo* sp., *Petalostemum* sp., *P. occidentale, P. purpureum, Phacelia* sp., *Physostegia* sp., *P. parviflora, Platycodon grandiflorum, Pluchea camphorata, Prionopsis* sp., *Pycnanthemum flexuosum, P. pilosum, Pyrrhopappus multicaulis, Rudbeckia hirta, R. laciniata, R. triloba, Schrankia uncinata, Senecio* sp., *Silphium* sp., *S. integrifolium, S. laciniatum, S. perfoliatum, S. speciosum, Sium cicutaefolium, Solidago* sp., *S. canadensis, S. serotina, S. trinervata, Teucrium canadense, Verbena* sp., *V. hastata, V. stricta, Verbesina* sp., *V. encelioides, V. exauriculata, V. occidentalis, Vernonia* sp., *V. baldwini interior, V. fasciulata, Veronica* sp., *Vitex agnus-castus, Wislizenia refracta.*

Melissodes (Eumelissodes) trinodis Robertson

Melissodes trinodis Robertson, 1901, Canadian Ent., vol. 33, p. 231; 1905, Trans. Amer. Ent. Soc., vol. 31, p. 369; Graenicher, 1905, Bull. Wisconsin Nat. Hist. Soc., vol. 3, p. 164-165; 1911, Bull. Pub. Mus. Milwaukee, vol. 1, p. 247; Smith, 1910, Ann. Rept. New Jersey State Museum, p. 693; Robertson, 1914, Ent. News, vol. 25, p. 70; 1926, Psyche, vol. 33, p. 119; 1928, Flowers and Insects, p. 8; Pearson, 1933, Ecol. Monogr., vol. 3, p. 381; Graenicher, 1935, Ann. Ent. Soc. Amer., vol. 28, p. 304; Brimley, 1938, Insects of North Carolina, p. 463.

Melissodes pennsylvanica, Robertson, 1897, Trans. Acad. Sci. St. Louis, vol. 7, p. 355 (misidentification).

This species is closely related to *M. agilis.* The female of *trinodis* is very similar to that of *agilis,* differing chiefly in the darker color

as described below. The male can be separated from that of *agilis* by the piceous tergal margins, the black mandibular bases, the darker wing veins and the often less densely shagreened galeae.

Female. Measurements and ratios: N, 20; length, 10-12 mm.; width, 3.5-4.0 mm.; wing length, M = 3.45 ± 0.094 mm.; hooks in hamulus, M = 12.50 ± 0.224; flagellar segment 1/segment 2, M = 1.79 ± 0.023.

Structure and color: Integument black except as follows: apical half of mandible, distitarsus usually and flagellar segments 3 to 10 below rufescent; tegulae testaceous to piceous; eyes yellow to dark gray; wing membranes hyaline, veins dark reddish brown to black; tibial spurs yellow.

With structural characteristics of *agilis* except as follows: clypeus protruding beyond eye in profile usually by less than half width of eye, punctures round, regular, separated mostly by about half a puncture width; vertex with flattened lateral areas usually moderately shiny; maxillary palpal ratio about 4.25:3.50:3.75:1.00; galeae finely tessellate above; mesoscutum with punctures separated mostly by half a puncture width or less (including posteromedian area); mesepisternal punctures usually extremely shallow, surface dulled by fine, irregular shagreening; metasomal tergum 2 with interband zone punctures shallow, small, often absent at least; medially, separated mostly by more than one puncture width.

Hair: Color of vestiture as in *agilis* except as follows: labrum and apical half of clypeus often reddish brown; vertex usually with abundant dark brown hairs (occasionally all pale); head and thorax bright rufescent (rarely ochraceous); mesoscutum rarely with a few brown hairs in posteromedian area and scutellum occasionally with brown hairs medially; metasomal tergum 2 with interband zone hairs subappressed to erect, dark brown, apical area with short, appressed, relatively simple, dark brown hairs, distal pale band white and interrupted medially; tergum 3 with apical area as in tergum 2, distal pale band white and narrowly to broadly interrupted medially, rarely distal pubescent band all brown; tergum 4 brown at least in small apicomedian patch, often across all or most of apical margin of tergum and often interrupting distal pale band medially, occasionally tergum 4 all brown; terga 5 and 6 usually with pale lateral tufts but in darkest specimens all brown; sterna brown to dark brown except pale at extreme sides. Legs with hairs dark brown except as follows: femora yellow to rufescent; fore and middle tibiae and middle basitarsi often pale basally on outer

surfaces; tibiae with inner surfaces yellow to red; middle and hind basitarsi with inner surfaces dark red to brown; scopal hairs ochraceous to yellow except usually brown on and surrounding basitibial plates and near apices of basitarsi.

Male. Measurements and ratios: N, 20; length, 10-11 mm.; width, 3.5-4.0 mm.; wing length, M = 3.24 ± 0.152 mm.; hooks in hamulus, M = 11.25 ± 0.054; flagellar segment 2/segment 1, M = 9.06 ± 0.156.

Structure and color: Integment black except as follows: labrum with large mediobasal cream-colored macula; mandible rarely with small basal yellow macula; clypeus yellow; flagellar segments 2-11 red beneath, brown above; eyes green to yellowish brown or gray; wing membranes hyaline, colorless or slightly milky, veins reddish brown to black; tegulae usually piceous, occasionally testaceous; tarsi rufescent; tibial spurs white to yellow; apical margins of terga piceous to dark brown.

Structure as in *agilis* with the following differences: clypeus protruding beyond eye in profile by slightly less than half width of eye; minimum length of first flagellar segment equals one-seventh or less (often less than one-eighth) of maximum length of second segment; maxillary palpal ratio about 8:7:6:1. Sculpturing as in female except as follows: galeae above usually finely tessellate in apical half, often slightly so posteriorly, occasionally shiny except at tips; mesoscutal punctures often separated by more than half but less than one puncture width in posteromedian area; mesepisterna punctures usually deep, surface shiny to somewhat dulled by irregular shagreening; metasomal tergum 1 with basal five-sixths (medially) punctate, punctures smaller and sparser apically, in basal half separated mostly by half to one puncture width; tergum 2 with interband punctures distinct, separated by one to two puncture widths, apical area without distinct punctures; terga 3-5 similar to tergum 2 but interband punctures more regular in size, more crowded and smaller.

Sternum 7 similar to *agilis* but with median plate subtriangular, subequal or slightly larger than lateral plate in area, with ventral hairs minute. Sternum 8 as in *agilis* but ventral tubercle low, rounded, entire, with several short weak hairs at apex on either side of median emargination. Genital capsule as in *agilis* except as follows: gonostylus slender, indistinctly capitate, equal to about half length of gonocoxite, with short hairs laterally and minute hairs on inner surface (Figs. 76-77).

Hair: Color of vestiture as in female except as follows: without brown on clypeus, labrum or vertex; mesoscutum and scutellum without brown; terga 2-4 with apical areas with suberect brown hairs (often absent due to wear), distal pale bands usually complete but occasionally interrupted medially at least on tergum 4; tergum 5 often with a complete distal pale band, occasionally absent or broadly interrupted medially; terga 6 and 7 brown to almost black; sterna rufescent or golden medially and ochraceous to white laterally; legs with ochraceous hairs except inner surfaces of tarsi and hind tibiae yellowish. Thoracic and head hairs usually bright rufescent above and somewhat duller at sides, occasionally all thoracic and head hairs dull ochraceous.

Remarks. This bee resembles *M. agilis* very closely, especially in the female sex. It is quite possible that some paler females of *trinodis* have been identified as *agilis* or vice versa. That *trinodis* might be merely a variant of *agilis* appearing sporadically has been seriously considered. This hypothesis has been rejected on the basis that the males of *agilis* and *trinodis* are quite distinct and because *trinodis* does not appear west of the Great Plains where *agilis* is very abundant.

There is no uniform geographical variation in *trinodis* which could serve for the recognition of subspecies. However, females from the eastern seaboard, particularly from North Carolina, tend to be much darker in color than elsewhere in the range of the species. Some few females from this area resemble the females of *dentiventris* Smith and *bidentis* Cockerell (see below) on this account.

Bionomics. The only observations on the nesting habits of this species were published by Graenicher (1905, pp. 164-165). Graenicher briefly describes the nest of *M. trinodis* in connection with his studies of bee parasites and, in particular, in connection with the bee *Triepeolus helianthi* Robertson which was found parasitizing *M. trinodis.* Graenicher states, ". . . a ground inhabiting bee digs down perpendicularly to a depth of 8 cm., then turns off obliquely for a short distance, and continues in a perpendicular direction. The cells are somewhat thimble-shaped, their walls are formed of hardened clay with a very smooth and polished inner surface. They are filled about one-half with bee-bread." Graenicher observed *Triepeolus helianthi* entering the *M. trinodis* nest and he opened the nest on the following day. He observed two cells, one unfinished, the other closed and showing a white, opaque

egg of the host, 3 mm. in length, on the surface of the bee-bread. Graenicher then describes the activities of the first and second stage larvae of *T. helianthi* and, although he later dug up an additional nest of *M. trinodis,* he records no additional observations on this bee.

In regard to flower preferences, Robertson (1926) regarded *M. trinodis* as an oligolege of *Aster,* Heliantheae and Heleniae. This is very nearly correct, although the data available to the present author suggests that the genus *Aster* and the tribe Heleniae are not preferred markedly more than many other composites which these bees visit. On the other hand, the tribe Heliantheae, and particularly the genus *Helianthus,* is of the greatest importance as a source of pollen. The bee would be better described as an oligolege of the Compositae and in particular of *Helianthus.* The data supporting these conclusions is summarized in Table V.

TABLE V. Summary of Floral Records for *Melissodes trinodis.*

Plant Data			Records of *M. trinodis*			
FAMILY	Number of genera	Number of species	Number of collections	Number of females	Number of males	Total number of bees
Compositae, other than *Helianthus*	9	15	28	13	88	101
Compositae, *Helianthus* spp.	1	6	34	30	26	56
Others (6)	6	6	7	4	5	9
Totals	16	27	69	47	119	166

Type Material. Lectotype female (Robertson No. 9513) collected on *Helianthus grosse-serratus,* September 20, 1890 by Charles Robertson at Carlinville, Illinois, and lectoallotype male (Robertson, 8197) taken on *Lepachys pinnata,* July 25, 1888 by Charles Robertson at Carlinville are in the collection of the Illinois Natural History Survey, Urbana. In addition nine female and three male paratypes collected by Charles Robertson at Carlinville are in the collections of the Illinois Natural History Survey.

Distribution. This species occurs throughout most of eastern United States from Kansas and North Dakota in the west to Maine and Georgia in the east and in southeastern Canada (Fig. 10).

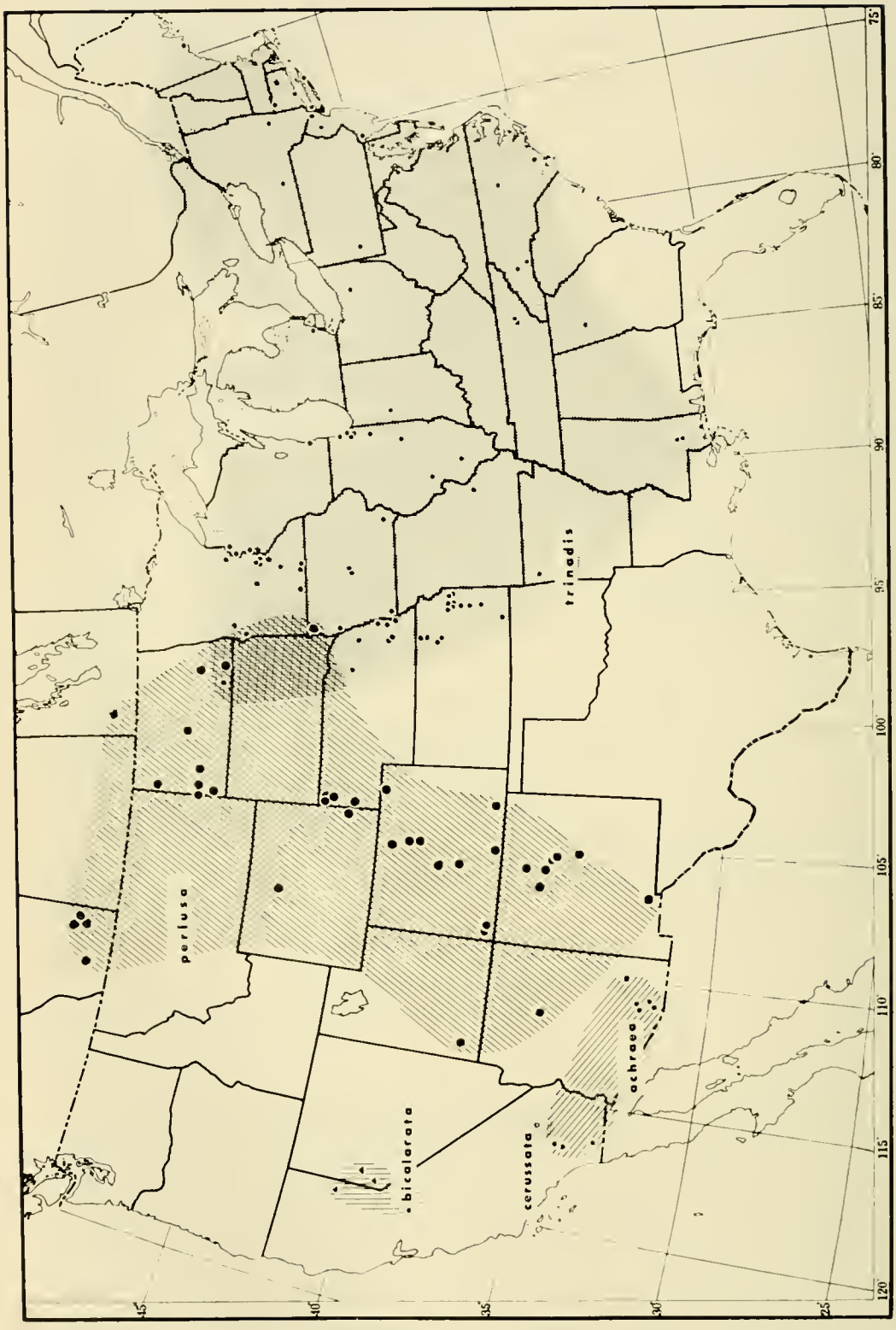


FIG. 10. Map showing the known distributions of *M. (Eumelissodes) trinodis* Robertson, *M. (E.) perlusa* Cockerell, *M. (E.) ochracea* LaBerge, *M. (E.) cerussata* LaBerge, and *M. (E.) bicolorata* LaBerge.

It has been collected between July 7 and October 23, but chiefly during August and September. In addition to the type material, a total of 116 females and 206 males from the localities listed below (including localities reported in the literature) have been examined.

Arkansas: Fayetteville. Connecticut: Colebrook; Storrs; Westville (New Haven). Georgia: Atlanta. Illinois: Beverly Hills; Carlinville; Chicago; Dubois; Evanston; Kankakee; Palos Park; Urbana; West Pullman; Willow Springs. Indiana: "Ind." Iowa: Ames (3 miles N. and 6 miles W.); Farragut; Mt. Pleasant (6 miles S. W.); Sioux City. Kansas: Allen Co.; Baldwin; Baldwin Junction; Blue Rapids; De Soto; Douglas Co.; Franklin Co.; Garnett; Lawrence; Manhattan; Marysville; Montgomery Co.; Olathe; Riley Co. Maine: Waldoboro. Massachusetts: Sherborn. Michigan: Detroit. Minnesota: Barrett; Big Stone Co.; Dakota Co.; Fairmont; Faribault; Freeborn Co.; Hayward; Howard Lake; Lake Vadnais, Ramsey Co.; Pine Co.; Powder Plant Woods, Ramsey Co.; St. Paul. Mississippi: Camp Shelby (near Hattiesburg), Hattiesburg. Missouri: Silver Spring. Nebraska: Lincoln; Louisville; Malcolm; Nebraska City; Neligh; Omaha; West Point. New Jersey: Chester; Ramsey; Salem Co. New York: Brooklyn; Ithaca; New Rochelle; New Baltimore; Quoque (Long Island). North Carolina: Bostic; Burgaw; Marion; Raleigh. North Dakota: Monango. Ohio: Barberton. Pennsylvania: Pittsburgh. Tennessee: Knox Co.; Knoxville. Virginia: Falls Church. Wisconsin: East Farmington; Hudson; Milwaukee; Randall; Yellow River (mouth of), Burnett Co.

Flower Records. Arctium sp., *Asclepias incarnata, Aster* sp.; *A. anomalus, A. praeatus, Bidens aristosa, B. laevis, Blephilia hirsuta, Carduus crispus, Cassia chamaecrista, Cirsium* sp., *C. lanceolatum, Coreopsis palmata, C. tripteris, Dichophyllum marginatum, Grindelia* sp., *Helenium altissimum, H. autumnale, Helianthus* sp., *H. annuus, H. annuus coronarius, H. atrorubens, H. divaricatus, H. grosse-serratus, H. maximillianus, H. mollis, H. salicifolius, H. tuberosus, Heliopsis helianthoides, Lepachys* sp., *L. pinnata, Liatris* sp., *Monarda fistulosa, Pepo* sp., *Petalostemum purpureum, Ratibida columnaris, Rudbeckia* sp., *R. hirta, R. laciniata, R. subtomentosa, R. triloba, Silphium* sp., *S. integrifolium, S. laciniatum, S. perfoliatum, Solidago* sp., *S. canadensis, S. rupestris, S. ulmifolia, Symphoricarpos* sp., *Teucrium canadense, Verbena* sp., *V. hastata, V. stricta, Vernonia* sp., *V. glauca, V. baldwini interior, Veronica* sp.

Melissodes (Eumelissodes) bidentis Cockerell

Melissodes bidentis Cockerell, 1914, Ann. Mag. Nat. Hist., ser. 8, vol. 14, p. 362; Stevens, 1951, Bull. North Dakota Agric. Exp. Sta., No. 14, p. 31.

This small bee is related to both *M. agilis* and *M. trinodis.* It is very similar in color to the darker specimens of *trinodis.* The female of *bidentis* can be distinguished from both *trinodis* and *agilis* by the shiny, unshagreened galeae, and from *agilis* and most specimens of *trinodis* by the lack of pale bands on the abdomen. The male of *bidentis* is similar to that of *trinodis* in having black mandibular bases and dark wing veins, but can be separated from the latter by the longer first flagellar segments and by the unshagreened galeae.

Female. Measurements and ratios: N, 20; length, 10-12 mm.; width, 4.0-4.5 mm.; wing length, $M = 3.36 \pm 0.130$ mm.; hooks in hamulus, $M = 12.10 \pm 0.216$; flagellar segment 1/segment 2, $M = 1.77 \pm 0.021$.

Structure and color: Integument black except as follows: apical half of mandible, flagellar segments 3-10 below, distitarsi, occasionally basitarsi, tibiae and femora, rufescent; eyes grayish green; wing membranes slightly infumate, yellowish, veins dark reddish brown to black; tegulae piceous; tibial spurs yellow.

Structure and sculpturing as in *agilis* except as follows: clypeus usually with median carina in apical half; supraclypeal area with small, round, scattered punctures, densely tessellate; galeae shiny, unshagreened except at extreme tips; maxillary palpal ratio about 2.67:2.33:2.67:1.00, last segment sometimes shorter; vertex with lateral flattened areas shiny; mesoscutum with round punctures smaller than in *agilis,* in posteromedian area separated by one to three puncture widths, surface dulled by fine reticular shagreening; scutellum with surface dulled by reticular shagreening; mesepisterna with large, shallow punctures separated by half to one puncture width, surface shiny; metasomal tergum 1 with basal two- to three-fifths with small shallow punctures separated by one to two puncture widths, apical area impunctate, surface dulled by reticulotransverse shagreening; terga 2-4 as in *agilis* but punctures (especially in interband zone) smaller, sparser, and shallower and shagreening coarser.

Hair: Head pale rufescent with abundant dark brown on vertex and labrum and often with clypeus all or partly brown. Thorax above dark ochraceous to bright rufescent, laterally ochraceous to rufescent except dark brown on anterior and lower lateral surfaces

of mesepisterna. Metasoma dark brown to black except as follows: tergum 1 with long ochraceous hairs basally; tergum 2 with basal zone pubescence ochraceous; often some pale hairs on lateral surfaces of terga 2 to 4. Legs dark brown except as follows: inner surfaces of basitarsi and often distitarsi dark reddish brown to black; scopal hairs ochraceous except brown on distal part of basitarsi and on and surrounding basitibial plates.

Male. Measurements and ratios: N, 16; length, 10-11 mm.; width, 3.5-4.0 mm.; wing length, $M = 3.08 \pm 0.135$ mm.; hooks in hamulus, $M = 10.81 \pm 0.136$; flagellar segment 2/segment 1, $M = 5.21 \pm 0.093$.

Structure and color: Integumental color as in *trinodis* except as follows: flagellar segment 2 usually dark brown; metasomal terga with apical areas infumate but usually slightly translucent, brown.

Structure as in *trinodis* except as follows: minimum length of first flagellar segment equals one-fifth or more of maximum length of second segment; maxillary palpal ratio about 3:3:2:1. Sculpturing as in female except as follows: supraclypeal area often impunctate but densely tessellate; mesoscutum and scutellum with punctures slightly larger, more crowded, surface moderately shiny, less dulled by shagreening; mesepisterna with punctures deeper; metasomal tergum 1 with basal three- to four-fifths punctate, punctures basally large, distinct, separated by one to three puncture widths; terga 2-5 as in terga 2-4 of female but apical areas impunctate.

Sternum 7 as in *trinodis* but median plate somewhat larger relative to lateral plate. Sternum 8 as in *trinodis* but medioventral tubercle pointed. Gonostylus short, broad, indistinctly capitate, with sparse minute hairs basolaterally; gonocoxites with mediodorsal margins forming a semicircle basad of spatha due to somewhat produced tubercle at margin of each gonocoxite just basad of either end of spatha; spatha just or slightly less than twice as broad as long, without well-defined apicomedial emargination; penis valve narrow, with lateral process short and blunt (Figs. 78-79).

Hair: Head and thorax ochraceous to bright rufescent, usually rufescent above. Metasomal tergum 1 ochraceous basally and laterally to apical margin, apicomedially with short, suberect, dark brown hairs; tergum 2 with basal pubescence ochraceous to white, distal pale band extremely narrow, usually interrupted medially, not connected at sides to basal pale band, separated from apex of tergum laterally by about length of pale band, interband zone with suberect to erect, short, dark brown hairs, apical area with short,

subappressed to appressed, simple, dark brown hairs (often worn away); terga 3-5 similar to tergum 2 but basal tomentum dark brown and distal pale band often more broadly interrupted (on tergum 5 usually and tergum 4 occasionally distal pubescent band brown); terga 6 and 7 brown; sterna yellow to brown medially, pale laterally; legs with ochraceous to yellow hairs except inner surfaces of basitarsi and often distitari yellow to orange.

Remarks. As in the case of most species of *Eumelissodes*, *M. bidentis* is an oligolege of the Compositae and seemingly depends primarily upon plants of the tribe Heliantheae. However the data is at present extremely sparse.

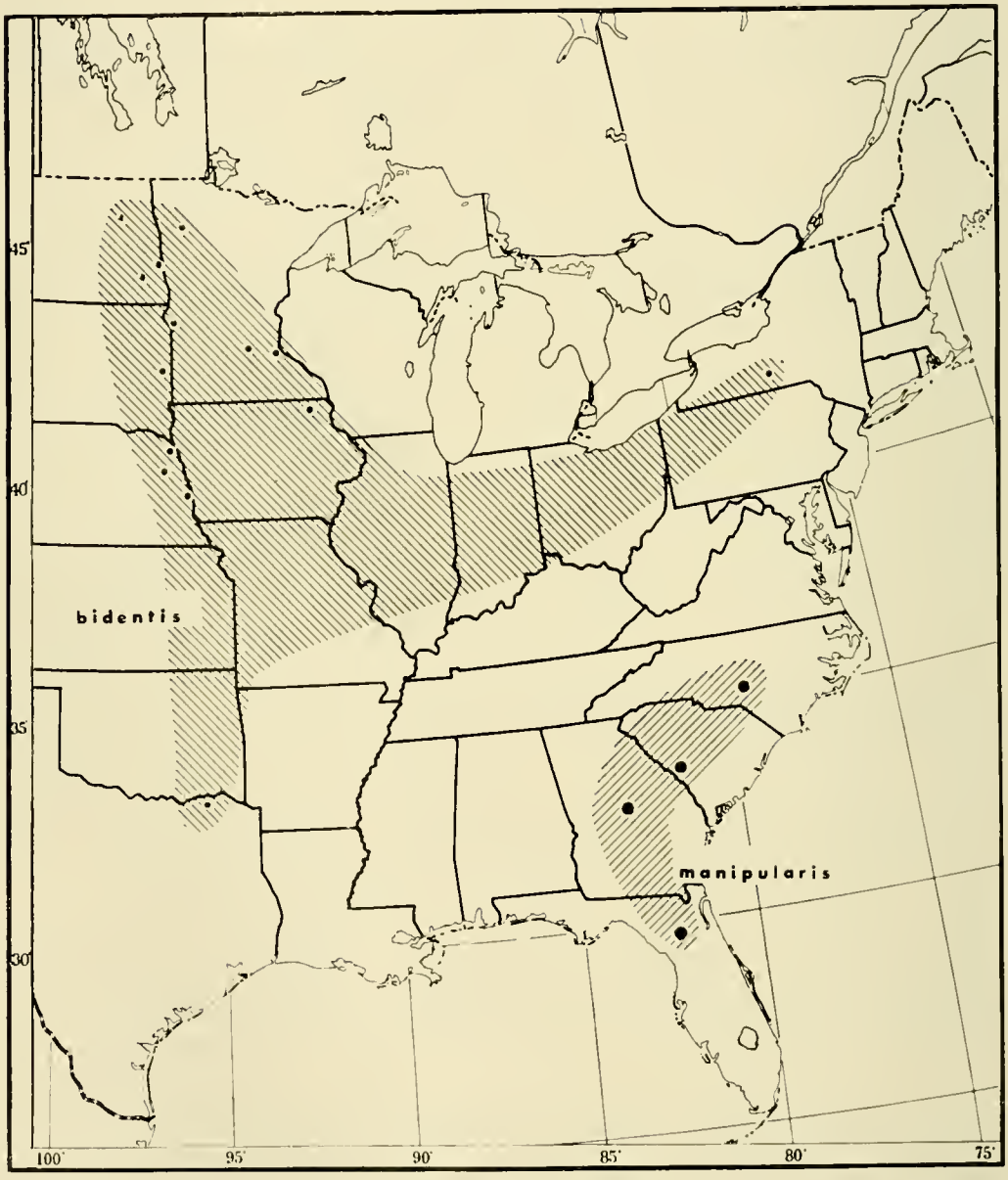


FIG. 11. Map showing the known distributions of *M. (Eumelissodes) bidentis* Cockerell and *M. (E.) manipularis* Smith.

Type Material. The holotype female of *bidentis* collected at West Point, Nebraska, September 21, 1903, on *Bidens* sp. by J. C. Crawford is in the U. S. National Museum (U. S. N. M. Type No. 22913). I have also examined one paratype with the same data as the holotype except that it was collected on September 22, 1903, which is in the American Museum of Natural History, New York City.

Distribution. The known range of *bidentis* extends from North Dakota to Texas and east to western New York State (Fig. 11). This species has been collected from July 16 to October 8. A total of 26 females and 16 males have been examined (including the holotype) from the localities listed below.

Iowa: Decorah. Minnesota: Big Stone Co.; Carver Co. (Zumbro Heights); Hastings; Plummer. Nebraska: Omaha; South Sioux City; West Point. New York: Ithaca. North Dakota: Fargo; Lakota; Sheldon. South Dakota: Brookings. Texas: Paris.

Flower Records. Bidens sp., *Echinacea pallida, Gossypium herbaceum, Helianthus annuus, H. maximillianus, H. tuberosus, Physostegia parviflora, Rudbeckia* sp., *R. laciniata, Sonchus arvensis.*

Melissodes (Eumelissodes) dentiventris Smith

Melissodes dentiventris Smith, 1854, Cat. Hymen. in Coll. British Mus. Part II. Apidae, p. 321; Robertson, 1894, Trans. Acad. Sci. St. Louis, vol. 6, pp. 463, 467, 469-471, 473-476; 1896, Trans. Acad. Sci. St. Louis, vol. 7, pp. 176-178; 1897, Trans. Acad. Sci. St. Louis, vol. 7, p. 355; 1898, Trans. Acad. Sci. St. Louis, vol. 8, p. 53; 1901, Canadian Ent., vol. 33, p. 230; 1902, Canadian Ent., vol. 34, p. 49; Smith, 1910, Ann. Report New Jersey State Mus., 1909, p. 693; Viereck, 1916, Connecticut St. Geol. and Nat. Hist. Surv. Bull. No. 22, p. 732; Cockerell, 1917, Canadian Ent., vol. 49, p. 212.

Melissodes autumnalis Robertson, 1905, Trans. Amer. Ent. Soc., vol. 31, p. 369; Cockerell, 1906, Trans. Amer. Ent. Soc., vol. 32, p. 114; Robertson, 1914, Ent. News, vol. 25, p. 70; 1926, Psyche, vol. 33, p. 119; 1926, Ecology, vol. 7, p. 379; 1928, Flowers and Insects, p. 8; Brimley, 1938, Insects of North Carolina, p. 462; Michener, 1947, Amer. Midl. Nat., vol. 38, p. 453.

Melissodes megacerata Cockerell, 1906, Ann. Mag. Nat. Hist., ser. 7, vol. 17, p. 362 (new synonymy).

The female of *dentiventris* resembles closely the darkest female of *trinodis* and those of *bidentis.* The female of *dentiventris* can be separated from those of the latter two species by its flatter clypeus which is more closely allied with the paraocular carina laterally, by its densely tessellate galeae and by its more coarsely punctured metasoma as described below. The male is distinguished by usually lacking pale pubescent bands on the metasomal terga (a complete band is present only on tergum 2 of some specimens),

the dulled galeae, the extremely short first flagellar segment, and by the black mandibles and labrum (often posterior part of clypeus is also darkened).

Female. Measurements and ratios: N, 20; length, 12-14 mm.; width, 4.5-6.0 mm.; wing length, M = 4.18 ± 0.058 mm.; hooks in hamulus, M = 14.75 ± 0.064; flagellar segment 1/segment 2, M = 1.74 ± 0.015.

Structure and color: Integument black except as follows: apical half of mandible, lower surface of flagellar segments 3-10 and distitarsi rufescent; eyes gray to blue; wing membranes slightly infumate, yellow, veins dark reddish brown to black; tegulae piceous; tibial spurs usually reddish brown.

Clypeus flat, extreme lateral margin separated from eye margin by less than half minimum diameter of first flagellar segment, with coarse round punctures separated by half a puncture width or less, with well-marked median carina in apical half, surface slightly dulled by reticular shagreening; supraclypeal area usually impunctate and shiny medially; flattened lateral areas of vertex with round deep punctures separated by half to one puncture width, surface shiny; galeae above dulled by fine tessellation; maxillary palpal ratio about 2.50:2.67:2.50:1.00, rarely with minute fifth segment. Mesoscutum with large, deep, round punctures separated mostly by half a puncture width (by less in posteromedian declivous area), surface shiny; scutellum similar; mesepisternum with punctures similar in size and spacing to middle of mesoscutum, surface shiny; propodeum with dorsal surface reticulorugose basally and punctate apically, lateral and posterior surfaces coarsely punctate, surfaces dulled by dense, coarse tessellation. Metasomal tergum 1 with basal three-fourths with deep round punctures separated mostly by half to one puncture width, apical area impunctate, surface moderately shiny, with reticulotransverse shagreening (especially basally); tergum 2 with basal area with small deep punctures separated mostly by half a puncture width or less, interband zone with larger, shallow punctures separated mostly by one to two puncture widths, apical area with small punctures two to three times width of hairs arising from them, surface shiny to moderately so, shagreening extremely fine; terga 3 and 4 similar to tergum 2 but punctures of interband zones more crowded; pygidial plate broadly V-shaped with rounded apex.

Hair: Head usually ochraceous with abundant dark brown on vertex, often with dark brown mixed with pale on clypeus and on

frons down to level of antennal fossae, rarely most of head hairs dark. Thorax dark ochraceous to bright rufescent above and on upper half of lateral surfaces, rarely with a few dark brown hairs in posteromedial area of mesoscutum and medially on scutellum, anteriorly and lower lateral surfaces dark brown; tegulae dark brown at least posteriorly. Metasomal vestiture usually entirely dark brown to black except ochraceous (or ochraceous and dark mixed) on basal half of tergum 1 and ochraceous pubescence at extreme base of tergum 2; occasionally tergum 2 with thin distal pubescent band also ochraceous or ochraceous laterally; rarely tergum 3 with distal pubescent band light brown or dark ochraceous laterally. Legs dark brown to black except as follows: inner surfaces of fore and middle tarsi and tibiae reddish brown, inner surfaces of hind bastitarsi often dark reddish brown, scopae yellow to ochraceous except brown at apices of basitarsi and on and surrounding basitibial plates.

Male. Measurements and ratios: N, 20; length, 10-13 mm.; width, 3.5-5.0 mm.; wing length, M = 4.12 ± 0.188 mm.; hooks in hamulus, M = 13.60 ± 0.234; flagellar segment 2/segment 1, M = 9.61 ± 0.281.

Structure and color: As in female except as follows: clypeus yellow, often dark brown along posterior margin, rarely brown except median one-third; flagellar segments 2-11 yellow to red below; apices of metasomal terga often slightly translucent; tibial spurs usually yellow.

Structure as in female with following differences: minimum length of first flagellar segment usually subequal to pedicel and equal to about one-tenth of maximum length of second segment; maxillary segments in ratio of about 2.0:2.5:2.0:1.0, rarely with fifth segment; basitibial plate rounded apically. Sculpturing as in female except as follows: clypeal punctures less distinct; metasomal tergum 1 with basal four-fifths punctate; terga 3-5 similar to tergum 2 but interband zone punctures smaller and more crowded, apical areas less distinctly punctured than in female.

Sternum 7 as in *agilis* but with median plate subequal to slightly larger than lateral plate in area, with abundant minute hairs ventrally becoming long and coarse basally, and with a few minute, curled hairs directed inwards from dorsum of inner basal angle. Sternum 8 as in *agilis* but ventral tubercle strong and acute. Genital capsule as in *agilis* except as follows: gonostylus equals about half of gonocoxite in length, short, thick hairs basally on ventral surface

with tips split into two or three minute tines; gonocoxite with spicules of inner upper surface half hairlike and half short blunt structures (Figs. 80-81).

Hair: Head ochraceous to rufescent (especially on vertex). Thorax pale ochraceous to yellow laterally and ochraceous to bright ferrugineous above. Metasomal tergal vestiture dark brown except as follows: basal half or more of tergum 1 with long pale hairs (reaching apical margin at extreme sides); tergum 2 with basal pubescence pale, distal pubescent band narrow, often white at least in lateral thirds and occasionally across entire tergum; tergum 3 with distal pubescent band occasionally pale laterally; terga 2 and 3 and often 4 with pale hairs along extreme sides. Legs pale ochraceous to yellow except as follows: inner surfaces of basitarsi dark red; inner surfaces of distitarsi and hind tibiae often yellowish red; basitibial plates often pale brown.

Bionomics. This species is, according to Robertson (1926), an oligolege of the composite tribes Astereae and Heliantheae. According to the data gathered from specimen labels, *dentiventris* is dependent primarily upon flowers of the tribe Astereae (and particularly upon the genus *Aster*) and only secondarily upon other composites. Out of a total of 39 collections (76 bees) with flower data attached, 24 collections (47 bees of which 44 are females) were from some species of the genus *Aster*. The other 15 collections (29 bees of which only 17 are females) were taken on seven other genera of composites and of these the genus *Chrysopsis* (Astereae) was the most important.

Type Material. The holotype male (No. 17.B.834) of *dentiventris* from Georgia is in the collection of the British Museum (Natural History) in London, England. The lectotype female (here designated) of *autumnalis* from Carlinville, Illinois, taken on *Aster ericoides villosus* on September 21, 1895, by Charles Robertson (Robertson No. 17,765), and the lectoallotype male (here designated) collected at Carlinville by Robertson (Robertson No. 18,-670) are in the collection of the Illinois Natural History Survey, Urbana, Illinois. In addition, 23 female and 18 male paratypes of *autumnalis* are also at Urbana. The male holotype of *megacerata* collected by G. Birkmann on October 13, 1897, at Fedor, Lee Co., Texas, is in the collection of P. H. Timberlake at the Citrus Experiment Station, Riverside, California.

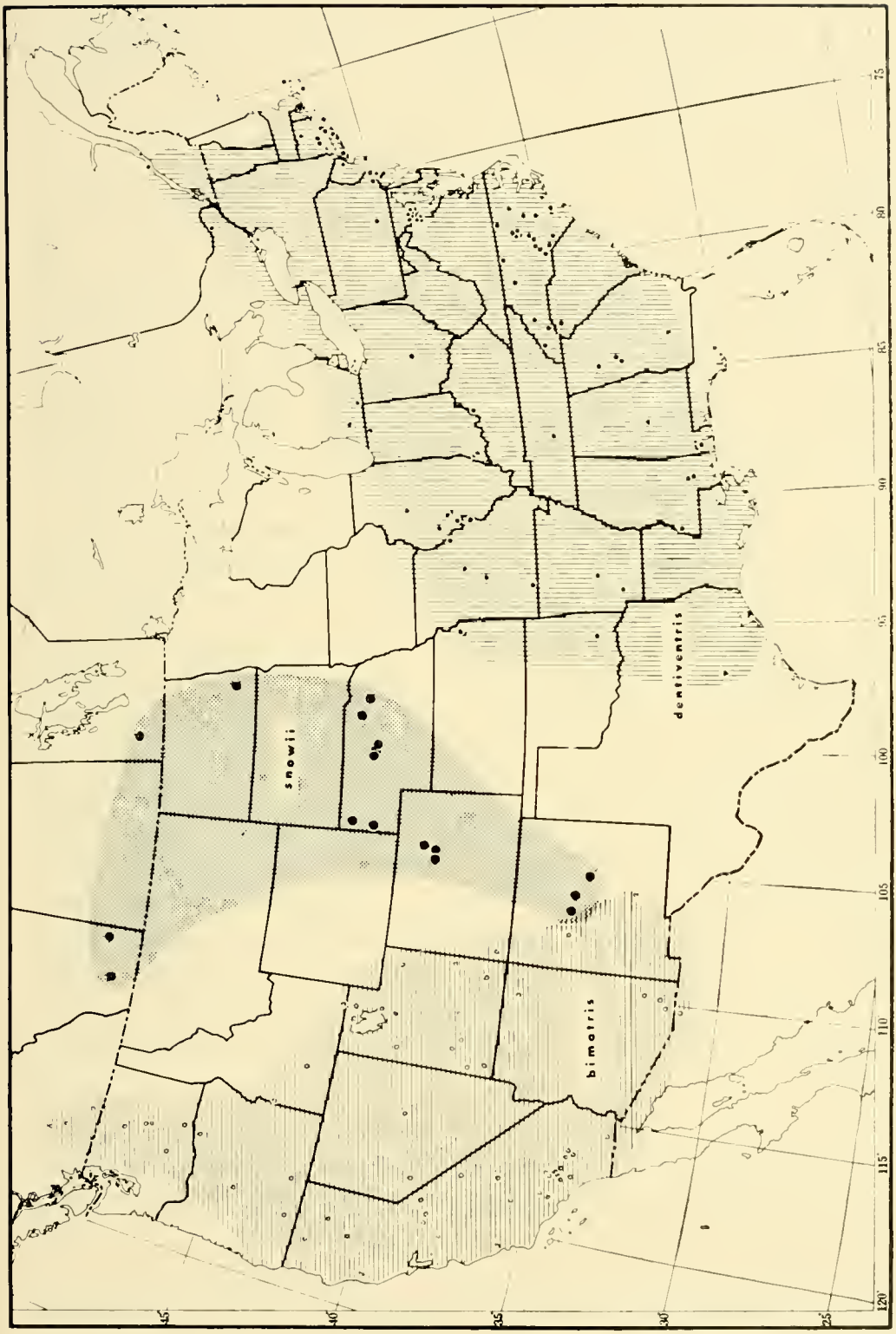


FIG. 12. Map showing the known distributions of *M. (Eumelissodes) dentiventris* Smith, *M. (E.) snowii* Cresson, and *M. (E.) bimatris* LaBerge.

Distribution. This species ranges from eastern Texas north to South Dakota and east to Georgia and southeastern Canada (Fig. 12). It has been collected from July 4 to October 27, but chiefly in September and October. In addition to the type material, 270 females and 108 males from the localities listed below have been examined. This list includes records reported in the literature.

ALABAMA: Kushla; Mobile; Saraland; Selma. ARKANSAS: Hope; Hot Springs. CONNECTICUT: Branford; Rockville; Westville. DISTRICT OF COLUMBIA: Washington. GEORGIA: Atlanta; Griffin; Neal Gap; Thomsons Mills; Tifton. ILLINOIS: Bluffs; Carlinville; Elsah, Jersey Co.; Macoupin Co.; Peoria. INDIANA: Elkhart; Gibson Co.; Rush Branch. KANSAS: Lawrence; Lone Star Lake, Douglas Co. KENTUCKY: Louisville. MARYLAND: Beltsville; Bethesda; Bladensburg; Cabin John; Glen Echo; Hyattsville. MASSACHUSETTS: Edgartown; Truro; Woods Hole. MICHIGAN: Hillsdale Co.; Kalamazoo Co. MISSISSIPPI: Camp Shelby (near Hattiesburg); Hattiesburg; Natchez. MISSOURI: Branson; Columbia; Louisiana; Ozark Lake; St. Louis. NEW JERSEY: Clementon; Da Costa; Gloucester Co.; Iona; Lakewood; Maplewood; Riverton. NEW YORK: Long Island (Bellmore; East Quoque; Flatbush; Greenport; Montauk; Northwest; Orient). NORTH CAROLINA: Black Mt.; Bryson City; Burgaw; Crabtree Creek State Park; Davidsons River; Faison; Harnett Co.; Lake View; Lumberton; Laurinburg; New River; Norlina; Pender Co.; Pikeville; Raleigh; Reidsville; Richmond Co.; Spout Spring; Southern Pines; Tarboro; Umstead State Park; Wake Co.; West Raleigh; Yadkin Co. OHIO: Franklin Co. OKLAHOMA: Tuskahoma. PENNSYLVANIA: Eberlys Mill; Philadelphia. SOUTH CAROLINA: Greenville. TENNESSEE: Maury Co. TEXAS: Fedor, Lee Co. VIRGINIA: Barcroft; Falls Church; Fort Humphreys; Fourmile Run (near mouth of). *Canada.* ONTARIO: Ottawa. QUEBEC: Cap Rouge.

Flower Records. Aster sp., *A. anomalus, A. dumosus, A. ericoides, A. ericoides villosus, A. novaeangliae, A. paniculatus, A. sagittifolius, A. turbinellus, Bidens aristosa, B. polylepis, Boltonia asteroides, Coreopsis tripterus, Chrysopsis* sp., *C. mariana, C. microcephala, Eupatorium perfoliatum, E. serotinum, Helianthus* sp., *H. annuus, H. divaricatus, H. grosse-serratus, H. radula, Isopappus divaricatus, Lespedeza virginica, Lippia lanceolata, Polygonum pennsylvanicum, Solidago canadensis, S. rigida, S. ulmifolia, Verbena hastata, Vernonia* sp., *Veronica* sp.

Melissodes (Eumelissodes) perlusa Cockerell

Melissodes semiagilis var. *perlusa* Cockerell, 1925, Ann. Mag. Nat. Hist., ser. 9, vol. 16, p. 231; 1926, Univ. Colorado Studies, vol. 16, p. 114.

The female of *perlusa* is similar to that of *agilis* but differs in that the lateral clypeal carina is closer to the eye, the metasomal terga are more finely punctate and the galeae are shinier. The female is also distinctive in having reddish wing veins, very pale vestiture and often red hairs on the inner surfaces of the hind basitarsi. The male of *perlusa* is similar to that of *agilis* except for the slightly longer first flagellar segment, the less coarsely punctate metasomal terga, the shiny galeae and the black mandibular bases.

Female. Measurements and ratios: N, 20; length, 12-14 mm.; width, 4.5-6.0 mm.; wing length, M = 3.88 ± 0.183 mm.; hooks in hamulus, M = 14.50 ± 0.212; flagellar segment 1/segment 2, M = 1.95 ± 0.029.

Structure and color: Integument color as in *agilis* except as follows: eyes greenish blue; apical area of tergum 1 usually translucent (even narrowly hyaline in some).

Sculpturing and structure as in *agilis* except as follows: clypeal punctures usually slightly smaller, crowded, apicomedial longitudinal carina usually present, protruding beyond eye in profile by less than half width of eye, lateral carina separated from eye margin by half or slightly more of minimum diameter of first flagellar segment; galeae above shiny, unshagreened or extremely delicately so; maxillary palpal ratio about 4.5:3.5:3.0:1.0; vertex with lateral flattened areas with minute punctures separated by one to three puncture widths, surface shiny. Mesoscutum as in *agilis* but punctures slightly larger, surface not shagreened; scutellar punctures smaller than mesoscutal. Metasomal tergum 1 with basal two-thirds or less punctate, punctures round, small, distinct, separated mostly by one puncture width, surface dulled by reticular shagreening (almost tessellate in appearance), apical area impunctate, moderately shiny, finely shagreened; tergum 2 with basal zone with minute round punctures separated by one to two puncture widths, surface dulled by dense tessellation, interband zone impunctate or with sparse punctures not much larger than base of hairs arising from them, surface dulled by tessellation, apical area impunctate or virtually so, surface dulled by coarse reticulotransverse shagreening; terga 3 and 4 similar to 2 but apical area of tergum 4 covered by distal pubescent band.

Hair: On head pale ochraceous to dark ochraceous, often yellow-

ish on vertex and occasionally vertex with sparse brown hairs. Thorax pale ochraceous or white laterally and posteriorly and dull ochraceous to dull rufescent (usually yellowish) above, without brown. Metasomal vestiture as in *agilis* except as follows: pale vestiture never rufescent, usually white to ochraceous; tergum 1 with apical area glabrous; tergum 2 with pale interband zone hairs never brown, erect to suberect, long, with distal pale band rarely interrupted medially, of about equal length across tergum and almost as long as apical area medially, with apical area hairs always pale ochraceous or white, suberect, distinctly plumose and more abundant than in *agilis;* tergum 3 as in tergum 2 but apical area narrower, basal tomentum brown and distal pale pubescence invading interband zone; tergum 4 as in *agilis* but distal pale band broader and never with minute apicomedian brown area; sterna yellow to pale brown medially, paler laterally. Legs pale ochraceous to white except as follows: outer surface of fore basitarsi, outer surface of apical area of middle tibiae and on and surrounding basitibial plates pale brown; inner surfaces of tarsi and hind tibiae yellow to dark reddish brown.

Male. Measurements and ratios: N, 20; length, 10-13 mm.; width, 3-4 mm.; wing length, $M = 3.49 \pm 0.197$ mm.; hooks in hamulus, $M = 12.95 \pm 0.223$; flagellar segment 1/segment 2, $M = 5.42 \pm 0.095$.

Structure and color: Integumental color as in *agilis* except as follows: mandibular bases without yellow spots; labrum with mediobasal pale spot present or absent; eyes yellowish green; tergal margins hyaline, colorless.

Structure as in *agilis* except as follows: clypeus protruding beyond eye in profile by less than half width of eye; first flagellar segment with minimum length equal to one-fifth or slightly more of maximum length of second segment, usually about one and one-half times as long as pedicel on that side; maxillary palpal ratio about 7:4:4:1, last segment often shorter. Sculpturing as in female except as follows: clypeal punctures less distinct; supraclypeal area often shiny; galeae usually unshagreened, or with delicate reticular shagreening.

Sternum 7 as in *dentiventris* but median plate with basoventral hairs more slender and sparser, median plate slightly larger than lateral plate. Sternum 8 as in *agilis*. Genital capsule as in *agilis* but hairs of gonostylus and gonocoxite as in *dentiventris* although sparser and more slender.

Hair: Head and thorax white to pale ochraceous, often slightly darker on upper surface of thorax and on vertex. Metasomal terga as in *agilis* but pale vestiture always white to extremely pale ochraceous, vestiture longer, terga 2-4 with suberect hairs of apical areas long and distinctly plumose, without brown. Legs white to pale ochraceous except inner surfaces of tarsi yellow to pale reddish yellow.

Bionomics. *M. perlusa* is probably an oligolege of the genus *Helianthus.* Too few collections with flower data are available to arrive at a definite conclusion. Of 38 collections (58 bees) available with flower data, 23 collections (12 females and 28 males) were made on some species of *Helianthus* (the majority on *H. petiolaris*). Of the remaining 15 collections (18 bees), 8 (7 females and 3 males) were made on some other composite and 7 (4 females and 4 males) were made on either legumes or labiates.

Type Material. The holotype male of *perlusa* from Mesa Verde, Colorado, July 3-7, 1919, is in the collection of the American Museum of Natural History in New York City. Two paratype males with the same locality data are in the collection of P. H. Timberlake at the Citrus Experiment Station, Riverside, California.

Distribution. *M. perlusa* ranges from Arizona and New Mexico north to Alberta and Manitoba in the western prairies and eastern Rocky Mountains (Fig. 10). It has been collected from June 20 to September 26, but mainly in July and August. In addition to the holotype, 48 females and 49 males from the localities listed below have been examined.

Arizona: Flagstaff. Colorado: Alder; Berkley; Boulder; Clear Creek; Cortez; Golden; Larimer Co.; Mesa Verde; Peetz, San Luis Valley; Tobe. Iowa: Lyon Co. Nebraska: Glen, Sioux Co.; Harrison; Mitchell; Monroe Canyon, Sioux Co. New Mexico: Embudo; Jemez Springs; Las Cruces; Rowe; San Jose; Santa Fe; Vaugn. North Dakota: Beach; Dickinson; Marmarth; Medora; Nicholson; Valley City; Washburn; Williston. Utah: Kanarrville. Wyoming: Torrington; Worland. *Canada.* Alberta: Lethbridge; Medicine Hat; Suffield; Whitla. Manitoba: Aweme.

Flower Records. *Biglovia* sp., *Brauneria pallida, Grindelia* sp., *Helianthus* sp., *H. annuus, H. petiolaris, Lepachys* sp., *Medicago sativa, Mentha canadensis, Petalostemum* sp., *P. oligophyllum, Ratibida columnaris.*

Melissodes (Eumelissodes) snowii Cresson

Melissodes snowii Cresson, 1872, Proc. Acad. Nat. Sci. Philadelphia, vol. 24, p. 211; Robertson, 1898, Trans. Acad. Sci. St. Louis, vol. 8, p. 53; Bridwell, 1899, Trans. Kansas Acad. Sci., vol. 16, p. 211; Cockerell, 1906, Trans. Amer. Ent. Soc., vol. 32, p. 76; Tucker, 1909, Trans. Kansas Acad. Sci., vol. 22, p. 281; Cresson, 1916, Mem. Amer. Ent. Soc., vol. 1, p. 130.

This species is extremely close to *M. perlusa* Cockerell. The female of *snowii* is similar to that of *perlusa* in most respects; however, *snowii* females have slightly more distinct punctures in the interband zone of tergum 2, often darker hairs on the inner surfaces of the hind basitarsi, more distinctly sculptured galeae and shorter and less plumose hairs in the apical areas of terga 2 and 3. The males of *snowii* are readily distinguished from those of *perlusa* by the yellow mandibular bases. They can be separated from the palest males of *agilis* only with difficulty, but the extremely short first flagellar segment and the white vestiture are distinctive. The males also resemble the males of *M. nivea* Robertson as discussed in the diagnosis of that species.

Female. Measurements and ratios: N, 20; length, 12-13 mm.; width, 3.5-4.5 mm.; wing length, $M = 3.35 \pm 0.116$; hooks in hamulus, $M = 12.85 \pm 0.608$; flagellar segment 1/segment 2, $M = 1.86 \pm 0.022$.

Structure and color: Integumental color as in *perlusa* except eyes usually blue, gray or greenish blue. Sculpturing and structure as in *perlusa* except as follows: lateral clypeal carina separated from eye margin by more than half and usually by one-third to three-fourths minimum diameter of first flagellar segment; galea above dulled by fine, dense tessellation; maxillary palpal ratio about 3.2:3.2:3.2:1.0; mesoscutal punctures often slightly larger and sparser in posteromedian area; metasomal tergum 1 with basal three-fourths or less with punctures separated mostly by half to one puncture width, surface shiny with coarsely reticular shagreening, interband zone with small shallow punctures separated mostly by two to three puncture widths, surface moderately shiny, apical area with minute punctures or impunctate, surface moderately shiny; tergum 3 as in tergum 2 but interband zone punctures more abundant and more distinct.

Hair: Head white, a few brown hairs often present on vertex. Thorax white, often extremely pale ochraceous above. Metasomal vestiture as in *perlusa* but pale vestiture always white, never ochraceous, apical areas of terga 2 and 3 with subappressed hairs simple or plumose only at extreme base, short and a few (especially on

tergum 3) often pale brown, and sterna brown except white laterally. Legs white except as follows: fore tarsi, outer surfaces of middle tibiae (near apices) and often basitarsi, and on and surrounding basitibial plates brown; scopae white to extremely pale ochraceous; inner surfaces of basitarsi and hind tibiae yellow to brownish red.

Male. Measurements and ratios: N, 20; length, 10-12 mm.; width, 3.5-4.0 mm; wing length, $M = 3.23 \pm 0.087$; hooks in hamulus, $M = 11.80 \pm 0.186$; flagellar segment 2/segment 1, $M = 10.24 \pm 0.188$.

Structure and color: Integumental color as in *perlusa* except as follows: mandibular bases with large yellow spots; labrum white except narrow brown apical margin (more than half of area pale); eyes bluish gray to greenish blue; tegulae usually piceous; wing veins yellow; flagellar segments 2 to 11 yellow below, red above.

Structure as in *perlusa* except as follows: first flagellar segment with minimum length to about one-tenth of maximum length of second segment and subequal to pedicel on same side; maxillary palpal ratio about 3:3:3:1. Sculpturing as in female except as follows: clypeus with punctures less distinct; galeae with tessellation finer, often shiny and unshagreened or tessellate except in apical third; mesoscutum with posteromedian area punctures often separated by 3 or more puncture widths; metasomal tergum 1 with basal four-fifths with punctures separated by half to one or slightly more puncture widths.

Sternum 7 as in *perlusa* with median plate with apical margin transverse and ventral hairs minute, sparse and more delicate mediobasally. Sternum 8 as in *agilis* but apical hairs minute and ventral tubercle usually not bidentate apically, cariniform. Genital capsule as in *agilis* but inner apical spicules of gonocoxite at least half short and blunt and gonostylus subequal to half of gonocoxite (Figs. 82-83).

Hair: Vestiture entirely white, rarely slightly grayish or yellowish on dorsum of thorax. Tergal vestiture as in *perlusa* except as follows: terga 2 and 3 with apical areas with suberect hairs long, white, simple except a few plumose at extreme bases; tergum 2 with distal pubescent band usually as long medially as apical area. Legs white except inner surfaces of basitarsi and often distitarsi yellow.

Bionomics. This bee is probably oligolectic on Compositae. The females have been collected most often on *Helianthus* and

Solidago, but there is not sufficient information for a more adequate statement of flower preferences. The only non-composite on which females have been taken is *Medicago sativa*.

Type Material. Lectotype male (No. 2330) and one male paratype collected by Snow in Colorado are in the collection of the Philadelphia Academy of Natural Sciences.

Distribution. M. snowii ranges over the western parts of the Great Plains from Alberta in the north to New Mexico in the south (Fig. 12). It has been collected from July 10 to September 18, but mostly during August. In addition to the type material, 30 females and 26 males have been examined from the localities listed below. A majority of these 56 specimens are from Halsey, Nebraska.

COLORADO: Boxelder Creek (E. of Aurora); Denver; Roggen. NEBRASKA: Dunning; Glen, Sioux Co.; Halsey; Holt Co.; Mitchell; Neligh; Thedford. NEW MEXICO: Albuquerque; Moriarity; Vaughn. NORTH DAKOTA: Sheldon. *Canada.* ALBERTA: Lethbridge; Seven-persons. MANITOBA: Aweme.

Flower Records. Aster sp., *Cleome serrulata, Gaillardia* sp., *Gutierrezia sarothrae, Helianthus* sp., *H. petiolaris, H. subrhomboideus, Lacinaria punctata, Medicago sativa, Solidago missouriensis, S. nemoralis, S. rigida.*

Melissodes (Eumelissodes) submenuacha Cockerell

Melissodes menuacha var. *submenuacha* Cockerell, 1897, Entomologist, vol. 30, p. 137; 1877, New Mexico Col. Agric. and Mech. Arts, Bull. No. 24, p. 28; 1898, Bull. Sci. Lab. Denison Univ., vol. 11, p. 66; 1898, Bull. Univ. New Mexico, vol. 1, p. 66; 1906, Trans. Amer. Ent. Soc., vol. 32, p. 309.
Melissodes hewetti Cockerell, 1905, Ann. Mag. Nat. Hist., ser. 7, vol. 15, p. 527 (new synonymy); 1906, Trans. Amer. Ent. Soc., vol. 32, pp. 84, 86; 1906, Trans. Amer. Ent. Soc., vol. 32, p. 309.

This large pale species is very similar in appearance to *M. perlusa* Cockerell. The females of *submenuacha* can be separated from those of *agilis* by the coarser clypeal punctation and by the lateral clypeal carina being closer to the eye margin. They can be separated from the females of *perlusa* by the slightly larger size, the dark wing veins, the coarser clypeal punctures, the denser punctures of the basal area of tergum 2, and the usually shagreened surface of the mesoscutum. The males of *submenuacha* are similar to those of *perlusa* in the dark mandibular bases, the flatter clypeus, the less coarsely punctate terga and the shinier galeae, but differ from those of *perlusa* by the short first flagellar segment and the sculpturing of the mesoscutum and base of tergum 2 as described below.

Female. Measurements and ratios: N, 10; length, 13-15 mm.; width, 4.5-6.0 mm.; wing length, M = 4.54 ± 0.211 mm.; hooks in hamulus, M = 15.90 ± 0.100; flagellar segment 1/segment 2, M = 2.13 ± 0.032.

Structure and color: Integument black except as follows: mandible with apical half or more, usually apical margin of clypeus, flagellar segments 3-10, tarsi and often tibiae at least partly, occasionally apical areas of terga 2-4 rufescent; eyes grayish brown to grayish green; wing membranes colorless, veins dark reddish brown to black; tegulae testaceous, yellow to rufescent; tibial spurs yellow to red.

Structure and sculpturing as in *perlusa* except as follows: clypeus separated from eye margin laterally by about three-fourths minimum diameter of first flagellar segment, with coarse, irregularly round punctures separated mostly by half a puncture width or less, usually with longitudinal median carina in apical half or more, surface shiny, with sparse delicate cross-striations; supraclypeal area sparsely or not punctate medially, shiny, usually with coarse reticular shagreening; galeae usually with coarse reticular shagreening dulling apical half or more above; maxillary palpal segments in ratio of about 4.0:4.0:2.5:1.0; mesoscutum with posteromedian area with surface slightly dulled by coarsely reticular shagreening; metanotum and propodeum with reticulorugosity finer, tessellation coarser; metasomal tergum 1 with basal three-fifths with punctures separated by one to three puncture widths, surface with finely reticular shagreening; tergum 2 with basal area with minute punctures separated by half to one puncture width, apical area with surface somewhat dulled by fine reticulotransverse shagreening.

Hair: Head pale ochraceous to ochraceous (brighter on vertex), vertex often with sparse dark brown hairs. Thorax laterally and posteriorly white to pale ochraceous, ochraceous to yellow above, scutellum often with brown medially and mesoscutum rarely with a few brown hairs posteromedially. Metasomal vestiture as in *perlusa* except as follows: pale vestiture not usually white but pale ochraceous; tergum 2 with distal pale band much thinner medially than laterally (interrupted when worn) and usually about one-half to three-fourths length of apical area medially; terga 2 and 3 with apical areas with subappressed to suberect hairs short, plumose only in basal half or less (seemingly simple except when highly magnified), often pale brown partially at least on tergum 3; tergum 4 with distal pale band extremely broad; terga 5 and 6 with median

dark hairs golden brown, yellow laterally; sterna golden medially to pale ochraceous laterally. Legs as in *perlusa* except scopae pale yellow to pale ochraceous.

Male. Measurements and ratios: N, 20; length, 12-14 mm.; width, 4-5 mm.; wing length, M = 4.14 ± 0.170 mm.; hooks in hamulus, M = 14.15 ± 0.287; flagellar segment 2/segment 1, M = 7.33 ± 0.105.

Structure and color: Integumental color as in *agilis* except as follows: mandibular bases without yellow; labrum with or without mediobasal pale spot; first flagellar segment usually wholly dark brown; eyes yellow to yellowish green; tergal margins extremely broadly hyaline (apical third or more of tergum 1 and almost half of terga 2 and 3), colorless or yellow; wing veins reddish brown to dark brown.

Structure as in *perlusa* except as follows: minimum length of first flagellar segment equals less than one-sixth (usually about one-seventh) of maximum length of second segment, usually longer than pedicel on same side; maxillary palpal segments in ratio of about 8:7:5:1, last segment often twice as long. Sculpturing as in female except as follows: supraclypeal area often unshagreened; mesoscutellar shagreening often absent or extremely fine; tergum 1 with basal five-sixths to four-fifths punctate.

Sternum 7 as in *snowii* but median plate with apical margin inclined towards midline. Sternum 8 and genital capsule as in *snowii.*

Hair: Head and thorax pale ochraceous to ochraceous, usually somewhat brighter on vertex and dorsum of thorax. Metasomal terga as in *perlusa* except as follows: vestiture usually pale ochraceous rather than white; terga 3-5 with interband zones with abundant, long, appressed pubescence (less abundant than in distal pubescent bands, however). Legs pale ochraceous to white except yellow on inner surfaces of tarsi.

Type Material. Cockerell did not specify a single holotype for *submenuacha* in his original description and none has been found in collections in this country. However, four males from "Las Cruces, N. M., 9-5" have been examined. These are presumably part of the original type series. One male has "*submenuacha* Ckll." on a second label written in Cockerell's distinctive handwriting. A second of these has a note in Cockerell's handwriting which records the characters which Cockerell published in the original description and a second note by Fox agreeing to the notes by

Cockerell. These males are evidently those cited by Cockerell as being collected by C. H. Townsend. That male labeled *submenuacha* Ckll. is hereby designated as the lectotype of *submenuacha*. The lectotype is in the collection of the Natural History Museum of the University of Colorado at Boulder.

It is interesting that although no males have been seen from Las Cruces collected by Cockerell on September 22nd, as he states in the original description, a single female of *submenuacha* from Las Cruces collected on *Helianthus annuus* (which is mentioned in the description) on September 22nd by Cockerell has been examined. Another label on this specimen reads "*submenuacha* n. sp." Could Cockerell have recorded this female as a male in writing the description for publication? The holotype female of *hewetti* from Santa Fe, New Mexico, collected by T. D. A. Cockerell on *Cleome serrulata* in August is in the collection of P. H. Timberlake of the Citrus Experiment Station, Riverside, California.

Distribution. *M. submenuacha* is known from Arizona, New Mexico and western Texas (Fig. 13). It has been collected from May 11 to November 10, but chiefly in September. In addition to the holotype, 10 females and 22 males from the localities listed below have been examined.

Arizona: Cameron (19 miles W.); Cochise Co.; Douglas; Madera Canyon, Santa Rita Mts.; Nicks (Huachuca Mts.); Portal (3, 5 and 10 miles E.); Sabino Canyon, Santa Catalina Mts.; Sedona (and 15 miles S.); Theba; Tucson. New Mexico: Albuquerque; Embudo; Hurley; Las Cruces; Santa Fe; Wilna. Texas: Big Bend State Park (Hot Springs); El Paso; Hueco Mts. (W. side of), El Paso Co.

Flower Records. *Aploppapus gracilis, Bidens* sp., *Cleome serrulata, Helianthus* sp., *Hymenothrix wislizeni, Isocoma heterophylla, Medicago sativa, Verbesina encelioides.* Although *submenuacha* is probably an oligolege of the Compositae, there is not sufficient evidence to make a more precise statement of its flower preferences at this time.

Melissodes (Eumelissodes) menuachus Cresson

Melissodes menuachus Cresson, 1868, Trans. Amer. Ent. Soc., vol. 1, p. 388; 1875, *in* Wheeler, Report Geog. Geol. Surv. west of 100th Meridian, vol. 5, p. 727; 1876, Proc. Davenport Acad. Nat. Sci., vol. 1, p. 209; Cragin, 1886, Bull. Washburn Coll. Lab. Nat. Hist., vol. 1, p. 211; Cockerell, 1893, Trans. Amer. Ent. Soc., vol. 20, p. 338; Fox, 1893, Proc. California Acad. Sci., ser. 2, vol. 4, p. 118; Townsend, 1896, Canadian Ent., vol. 28, p. 139; Cockerell, 1897, Entomologist, vol. 30, p. 138; 1897, Bull. Agric. Exp. Sta. New Mexico Coll. Agric. and Mech. Arts, no. 24, p. 19; 1898, Zoologist, p. 313; 1898,

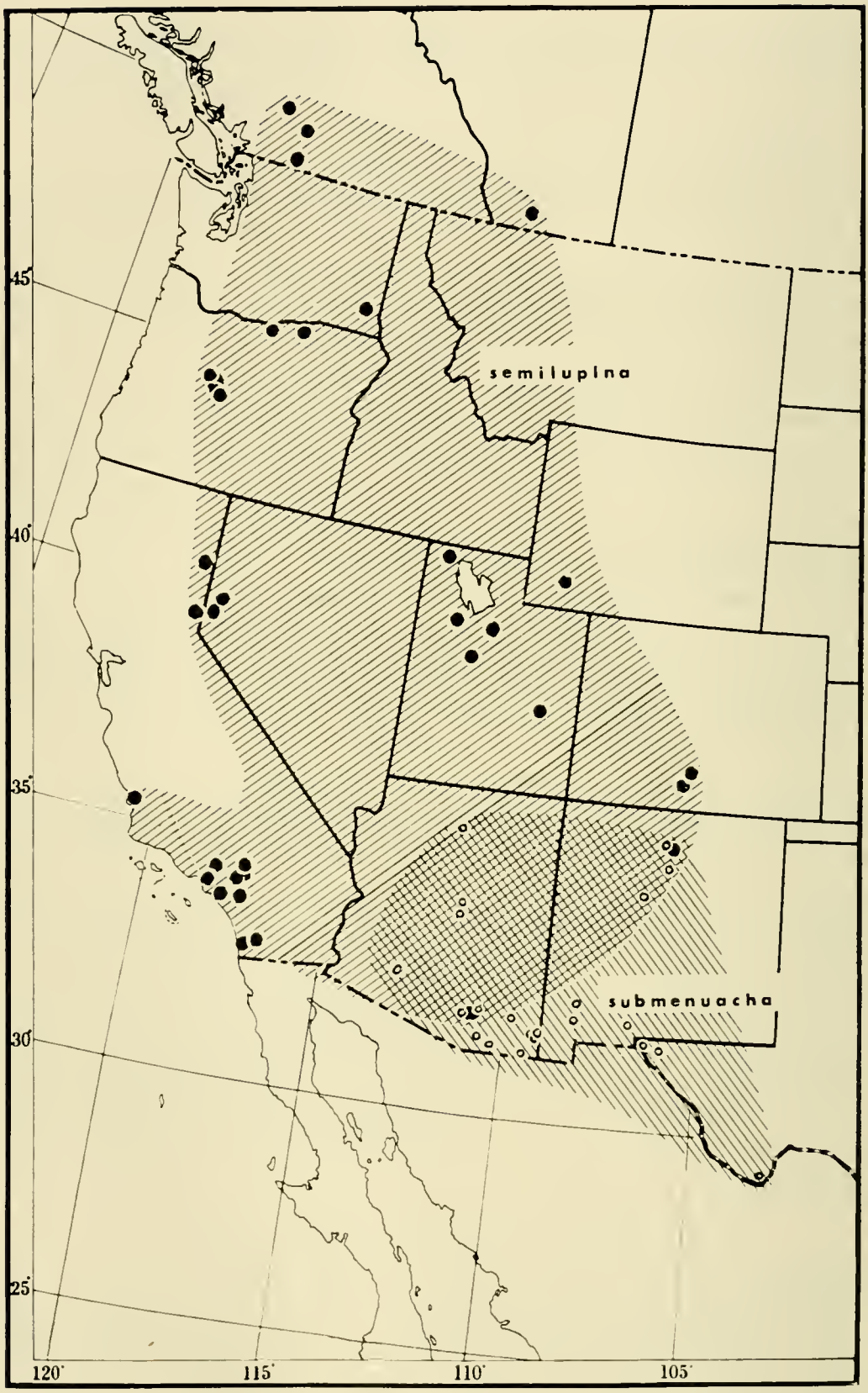


FIG. 13. Map showing the known distributions of *M. (Eumelissodes) semilupina* Cockerell and *M. (E.) submenuacha* Cockerell.

Bull. Univ. New Mexico, vol. 1, pp. 66, 67, 73; 1898, Bull. Sci. Lab. Denison Univ., vol. 11, pp. 66, 67, 73; 1899, Catalogo de las Abejas de Mexico, p. 14; Birkman, 1899, Trans. Kansas Acad. Sci., vol. 16, p. 211; Fowler, 1902, Univ. California Agric. Exp. Sta., p. 322; Cockerell, 1903, Psyche, vol. 10, p. 77; 1903, Ann. Mag. Nat. Hist., ser. 7, vol. 12, p. 449; Viereck, 1905, Canadian Ent., vol. 37, p. 320; Cockerell, 1906, Trans. Amer. Ent. Soc., vol. 32, pp. 77, 86, 92; 1906, Trans. Amer. Ent. Soc., vol. 32, p. 309; 1906, Bull. Amer. Mus. Nat. Hist., vol. 22, p. 443; Snow, 1906, Trans. Kansas Acad. Sci., vol. 20, p. 137; Tucker, 1909, Trans. Kansas Acad. Sci., vol. 22, p. 282; Smith, 1910, Ann. Rept. New Jersey State Mus., 1909, p. 693; Cockerell, 1910, Psyche, vol. 17, p. 246; 1910, Ent. News, vol. 10, p. 4; 1912, Proc. U. S. Nat. Mus., vol. 43, p. 271; Cresson, 1916, Mem. Amer. Ent. Soc., vol. 1, p. 123; Bray, 1917, Pomona Jour. Ent. Zool., vol. 9, p. 94.

Melissodes mennacus (!) Uhler, 1877, Bull. U. S. Geol., Geog. Surv., vol. 3, p. 783.

Melissodes pallida Robertson, 1895, Trans. Amer. Ent. Soc., vol. 22, p. 127 (new synonymy); 1905, Trans. Amer. Ent. Soc., vol. 31, p. 369; 1928, Flowers and Insects, p. 8.

Melissodes mizeae Cockerell, 1905, Ann. Mag. Nat. Hist., ser. 7, vol. 15, p. 522 (new synonymy); 1906, Trans. Amer. Ent. Soc., vol. 32, p. 86; 1906, Trans. Amer. Ent. Soc., vol. 32, p. 309; 1907, Univ. Colorado Studies, vol. 4, p. 255; Hicks, 1926, Univ. Colorado Studies, vol. 15, p. 225; Cockerell, 1933, Ann. Ent. Soc. Amer., vol. 26, p. 44.

Melissodes blakei Cockerell, 1905, Ann. Mag. Nat. Hist., ser. 7, vol. 15, p. 523 (new synonymy); 1906, Trans. Amer. Ent. Soc., vol. 32, p. 107; 1906, Trans. Amer. Ent. Soc., vol. 32, p. 309; 1927, Ann. Ent. Soc. Amer., vol. 20, p. 396.

Melissodes lavata Cockerell, 1924, Pan-Pacific Ent., vol. 1, p. 56 (new synonymy); 1927, Ann. Ent. Soc. Amer., vol. 20, p. 395; 1928, Univ. Colorado Studies, vol. 16, p. 114.

Melissodes octobris Cockerell, 1934, Ent. News, vol. 45, p. 30 (new synonymy).

This species is a large pale bee closely related to *M. submenuacha* Cockerell. The female of *menuachus* can be distinguished from any of the preceding species by the second flagellar segment being longer than broad and by the color of the vestiture as described below. The male of *menuachus* is similar in size to that of *submenuacha*, but has pale spots at the base of the mandible, as well as a pale labrum, and has the first flagellar segment longer in relation to the second segment.

Female. Measurements and ratios: N, 20; length, 13-16 mm.; width, 4.0-5.5 mm.; wing length, M = 4.56 ± 0.180 mm.; hooks in hamulus, M = 16.15 ± 0.254; flagellar segment 1/segment 2, M = 1.83 ± 0.016.

Structure and color: Integumental color as in *submenuacha* except as follows: eyes grayish blue to greenish gray; wing membranes slightly milky, veins red to reddish brown; tegulae usually testaceous.

Structure as in *agilis* except as follows: clypeus flat, protruding beyond eye in profile by one-third or less of eye width, with small, crowded, round punctures, surface dulled by coarse reticular shagreening, with distinct median longitudinal carina in apical half;

supraclypeal area shiny, often with coarse reticular shagreening but scarcely dulling surface; galeae shiny, with delicate shagreening above in apical half or less; maxillary palpal ratio about 5.0:4.5: 3.0:1.0, vertex with lateral flattened areas with minute sparse punctures, shiny; second flagellar segment ventrally slightly longer than broad. Mesoscutum with large deep punctures of rather variable diameter separated mostly by one-half to one puncture width, surface shiny; scutellum similar but punctures more crowded; mesepisternum with large shallow punctures separated mostly by much less than half a puncture width, surface shiny with extremely sparse and delicate shagreening. Metasomal tergum 1 with impunctate apical area expanded basally at sides to form two small, impunctate lateral lobes.

Hair: Head white except usually ochraceous on vertex. Thorax white to pale ochraceous laterally and posteriorly, bright to pale ochraceous above. Metasomal tergum 1 with basal area with long pale ochraceous hairs, apical area glabrous, pale basal hairs not reaching apical margin of tergum except at extreme sides; tergum 2 with basal white pubescence connected with distal pale band at sides, interband area with sparse, subappressed, relatively simple, pale hairs, distal pale band twice as long as apical apubescent area laterally, notched on posterior border at midline where usually half as long as apical area, apical area glabrous; tergum 3 similar to 2 but basal tomentum dark brown, distal pale band separated from apex by a narrow zone of suberect, pale relatively simple hairs, tergum 4 similar to 3 but apical suberect hairs absent; terga 5 and 6 brown except thick lateral white tufts; sterna brown medially to white at extreme sides. Legs white to pale ochraceous except as follows: fore tarsi, outer apex of fore and middle tibiae, on and surrounding basitibial plate, and inner surfaces of hind basitarsi brown to dark reddish brown; scopal hairs extremely long, usually pale yellow, occasionally pale ochraceous.

Male. Measurements and ratios: N, 20; length, 12-15 mm.; width, 3.5-5.0 mm.; wing length, $M = 4.22 \pm 0.181$ mm.; hooks in hamulus, $M = 14.25 \pm 0.239$; flagellar segment 2/segment 1, $M = 5.00 \pm 0.083$.

Structure and color: Integument black except as follows: clypeus and base of mandible yellow; labrum white except narrow apical margin brown; flagellum yellow to red below and brown to dark red above except first segment often entirely dark; eyes grayish yellow to greenish gray; distitarsi rufescent; wing membranes

hyaline, veins yellow to pale red; tegulae testaceous; apical areas of metasomal terga hyaline, colorless to yellow.

Structure as in *agilis* except as follows: minimum length first flagellar segment equals about two-thirds maximum length of first segment and about one-fifth (or slightly less) maximum length second segment; maxillary palpal ratio about 2.5:2.3:2.3:1.0; clypeus flat. Sculpturing as in female except as follows: galeae above shiny, with apical half often delicately shagreened; tergum 1 with basal four-fifths punctate, punctures usually somewhat larger, deeper and more crowded than in female; terga 3 and 4 with interband zone with small round punctures separated mostly by one to three puncture widths, occasionally mostly by one puncture width or less, surface dulled by coarse, reticular shagreening; tergum 5 similar but punctures more crowded.

Sterna 7 and 8 as in *submenuacha*. Genital capsule as in *submenuacha* but gonostylus with hairs on ventral surface near base short, stout, blunt, sparse, on outer lower surface mostly short, stout and bifid or trifid at apex; gonocoxite with several apical short, stout, blunt spicules on ventral surface below gonostylus in addition to those on inner apical surface (the latter are as in *submenuacha*).

Hairs: Head and thorax white to pale ochraceous, often brighter on vertex and dorsum of thorax. Metasomal tergum 1 with long white to ochraceous hairs basally, apically with long, appressed to subappressed pale hairs reaching margin of tergum (in fresh specimens) not obscuring apical area of tergum at least medially; tergum 2 with white pubescence basally, suberect, bristlelike, pale hairs in interband zone, white to pale ochraceous distal pubescent band not interrupted medially (unless worn) and separated from apical margin by one-half to one times length of pale band medially; terga 3-5 similar except interband zones with sparse, delicate, white, appressed pubescence in addition to bristlelike hairs and distal bands progressively closer to apical margin; terga 6 and 7 white to yellowish; sterna pale ochraceous to reddish medially, white laterally. Legs white to ochraceous except inner surfaces of tarsi golden yellow to pale rufescent.

Bionomics. Hicks (1926, p. 225) has recorded a few notes concerning the biology of *M. menuachus*. He discovered two females of *menuachus* nesting in the ground near Boulder, Colorado. On account of the condition of the soil, Hicks was unable to excavate these nests, although he did observe the females carrying pollen into their burrows. In both instances he observed a female of

Triepeolus occidentalis Cresson enter the burrow while the female *Melisssodes* was absent. Apparently *T. occidentalis* is a parasite of *M. menuachus* in that region.

M. menuachus is dependent upon flowers of the family Compositae and in particular upon the genera *Grindelia* and *Solidago*, according to the collection data available at this time. This is clearly shown in Table VI.

Type Material. The lectotype male of *menuachus* Cresson from New Mexico is in the collection of the Philadelphia Academy of

TABLE VI. Summary of Floral Records for *Melissodes menuachus.*

Plant Data			Records of *M. menuachus*			
FAMILY	Number of genera	Approximate number of species	Number of collections	Number of females	Number of males	Total number of bees
Compositae: *Grindelia* spp.	1	2	31	39	30	69
Compositae: *Solidago* spp.	1	3	14	17	6	23
Other Compositae	9	13	18	15	20	35
Leguminosae	3	3	7	3	4	7
Brassicaceae	1	1	6	0	9	9
Others (5)	5	5	8	2	8	10
Totals	20	27	84	76	77	153

Sciences. The holotype female of *pallida* Robertson, collected by Robertson (Coll. No. 9619) September 26, 1890, on *Helianthus grosse-serratus*, is in the collection of the Illinois Natural History Survey, Urbana. The holotype female of *mizeae* Cockerell, collected by Mize at Las Vegas, N. Mex., in August on *Grindelia inornata*, is in the collection of P. H. Timberlake, Citrus Experiment Station, Riverside, California. The holotype female of *blakei* Cockerell, collected at Beulah, N. Mex. in August, is in the collection of the U. S. National Museum (Type No. 40094). The female holotype of *lavata* Cockerell, collected at Wray, Colo., August 17-19, 1919, by F. Lutz, is in the collection of the American Museum of Natural History, New York City. The holotype female of

octobris Cockerell, collected at Hudson, Colo., October 1, 1933, is in the collection of P. H. Timberlake, Citrus Experiment Station, Riverside, California.

Distribution. This species is widely distributed from British Columbia, Alberta and North Dakota, east to Illinois and south to north-central Mexico and Texas (Fig. 14). It has been reported from Camden Co., New Jersey, by Smith (1910), but this is probably in error. It is most abundant in the prairie regions of Colorado, Nebraska and Kansas. *M. menuachus* has been taken from July 2 to October 6, but mainly in August and September. In addition to the types, a total of 245 females and 209 males from the localities listed below have been examined. This list includes localities reported in the literature.

ARIZONA: Bisbee (12 miles W.); Chiricahua Mts.; Flagstaff (and 7 miles S. and 4 miles N.); Mt. Graham; Grand Canyon;

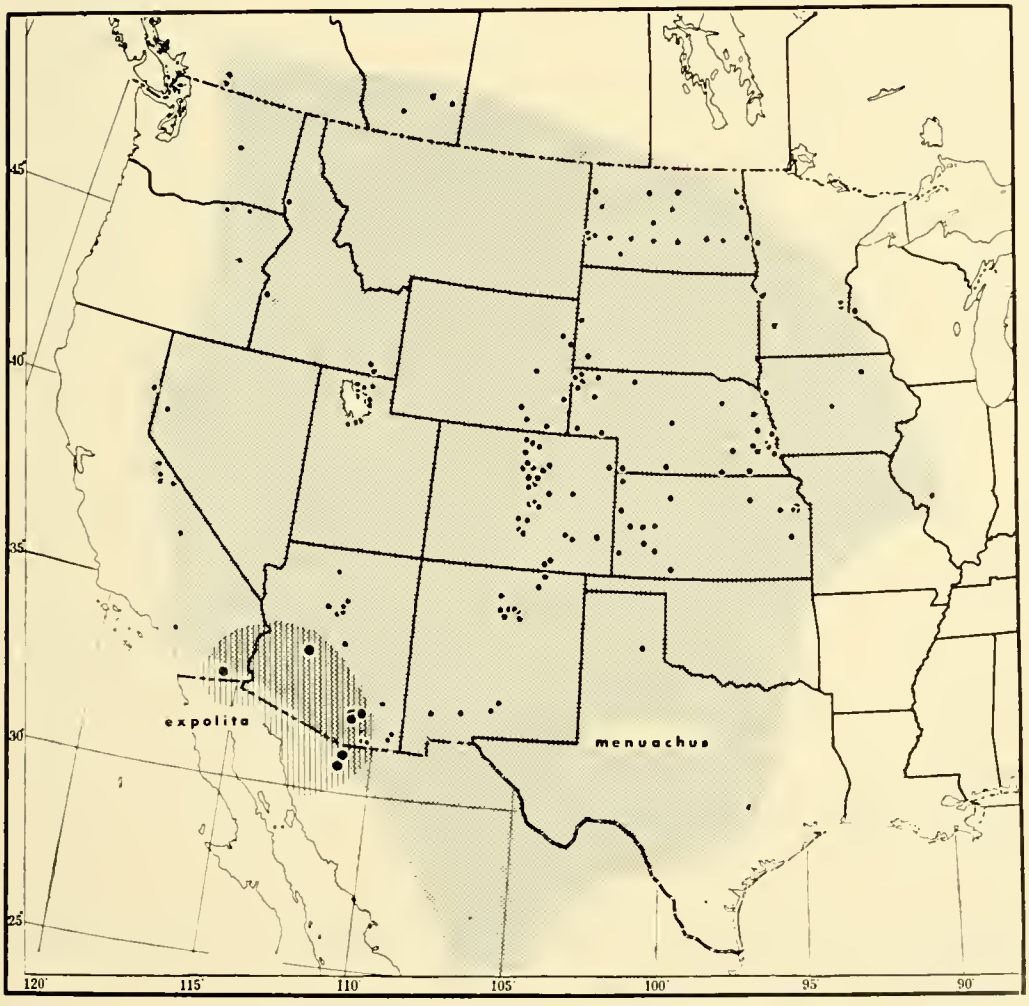


FIG. 14. Map showing the known distributions of *M. (Eumelissodes) menuachus* Cresson and *M. (E.) expolita* LaBerge.

Huachuca Mts.; Lochiel (4 miles E.); Payson; Sedona (10 miles N.); Southwest Research Station (5 miles W. of Portal); Williams. CALIFORNIA: Amedee, Lassen Co.; Benton's Crossing, Mono Co.; Bridgeport, Mono Co.; Grant Lake, Mono Co.; Mono Lake; Owen's Valley; Riverside. COLORADO: Boulder; Brighton; Buffalo Creek; Canon City; Chimney Gulch (near Golden); Colorado Springs; Custer Co.; Denver; Elbert; Eldora; Estes Park; Florissant; Fort Collins; Fremont Co.; Garden of the Gods (near Colorado Springs); Hoehne; Hudson; Jim Creek, Boulder Co.; La Junta; Lamar; Larimer Co.; Limon; Pingree Park; Platte Canyon (near Waterton); Poudre Canyon (W. of Fort Collins); Red Wash; Rock Creek (near Colorado Springs); Rocky Ford; Trinidad; West Cliff, Custer Co.; Wray. IDAHO: Downey; Franklin; Lewiston; Parma. ILLINOIS: Carlinville. IOWA: Ames; Chickasaw Co.; Sioux City. KANSAS: Baldwin; Cheyenne Co.; Clark Co.; Douglas Co.; Garden City; Garnett; Grant Co.; Hill City; Johnson (2 miles N.); Lane Co.; Lawrence; Riley Co.; Scott City (5 miles N.); Topeka; Wallace Co.; Wichita Co. MINNESOTA: Lyon Co.; Moorhead; Ortonville; Powder Plant Woods, Ramsey Co.; St. Paul. MONTANA: "Mon." NEBRASKA: Ashland; Box Butte Co.; Cambridge; Cedar Bluffs; Glen, Sioux Co.; Gordon; Haigler; Hardy; Harrison; Kimball; Lincoln; Lodgepole; Malcolm; McCool; Monroe Canyon, Sioux Co.; Nebraska City; Neligh; North Platte (8 miles W.); Omaha; Sand Hills, Cherry Co.; Sioux Co.; Steele City, Jefferson Co.; South Bend; West Point. NEVADA: Pyramid Lake. NEW MEXICO: Beulah; Embudo; Glorieta; Hurley (5 miles S.); Las Vegas; Maxwell City; Mescalero; Raton; Rincon; Rito de los Frijoles; Roziata; Tularosa Creek; Santa Fé; Sapello; Sapello Canyon. NORTH DAKOTA: Beach; Dickinson; Fargo; Glenn Ullin; Grafton; Grand Forks; Jamestown; Mandan; Martin; Medora; Minot; Mott; Rugby; Schafer; Sentinel Butte; Steele; Valley City; Washburn; Williston. OREGON: Echo; Freewater; Hereford. SOUTH DAKOTA: Deadwood; Hot Springs. TEXAS: Clarendon; Fedor, Lee Co. UTAH: Bear River City; East Promontory; Grantsville; Kaysville; Lake Point; Logan; Magna; Ogden; Promontory. WASHINGTON: Coulee City. WISCONSIN: Prescott. WYOMING: Albany Co.; Cheyenne; Clifton, Weston Co.; Douglas; Laramie; Torrington; Weston Co. *Canada.* ALBERTA: Lethbridge; Medicine Hat; Scandia. BRITISH COLUMBIA: Penticton; Similkameen. *México.* CHIHUAHUA: Aguascalientes (Sta. Barbara Dist.); Salaíces. ZACATECAS: Sain Alto.

Flower Records. Argemone sp., *A. intermedia, A. platyceras, Aster* sp., *A. laevis, A. multiflora, Cassia chamaecrista, Chrysopsis*

sp., *Chrysothamnus* sp., *C. graveolus glabrata, Cleome* sp., *C. serrulata, Eustoma russellianum, Gaillardia* sp., *Grindelia* sp., *G. inornata, G. squarrosa, Gutierrezia* sp., *G. californicum, G. sarothrae, Helianthus* sp., *H. annuus, H. petiolaris, Hymenothrix wislizenia, Medicago sativa, Melilotus* sp., *M. alba, Petalostemum oligocephalum, Polygonum* sp., *Rudbeckia laciniata, Sidalcea neomexicana, Solidago* sp., *S. canadensis, S. rigida, Verbena* sp., *Viguiera* sp., *Xanthocephalum gymnospermoides.*

Melissodes (Eumelissodes) semilupina Cockerell

Melissodes menuacha semilupina Cockerell, 1905, Bull. S. California Acad. Sci., vol. 4, p. 29.
Melissodes chrysothamni Cockerell, 1905, Ann. Mag. Nat. Hist., ser. 7, vol. 15, p. 524, (new synonymy); 1906, Trans. Amer. Ent. Soc., vol. 32, p. 85; 1906, Trans. Amer. Ent. Soc., vol. 32, p. 309.
Melissodes mizeae, Cockerell, 1912, Ann. Mag. Nat. Hist., ser. 8, vol. 10, p. 448 (misidentification).

This species is a large bee closely related to *M. menuachus* Cresson. The female of *semilupina* agrees with *menuachus* in having a relatively long second flagellar segment. It differs, however, in lacking the pale lateral tufts of hairs on terga 6 and 7 and in having brown hairs on the anterior and lower-lateral parts of the mesepisterna and coxae. The male of *semilupina* resembles that of *menuachus* closely but has a distinct band of long, pale, appressed pubescence covering the apical margin of the first tergum.

Female. Measurements and ratios: N, 20; length, 13-16 mm.; width, 4.5-6.0 mm.; wing length, $M = 4.70 \pm 0.247$ mm.; hooks in hamulus, $M = 18.10 \pm 0.240$; flagellar segment 1/segment 2, (19) $M = 1.91 \pm 0.024$.

Structure and color: Integumental color as in *menuachus* except as follows: eyes grayish blue; second (often third) flagellar segment totally black, segments 3 to 10 usually dark red below; tegulae piceous; wing veins dark brown; apical areas of terga usually black, occasionally dark reddish brown.

Structure and sculpturing as in *menuachus* except as follows: length of second flagellar segment occasionally equal to width, usually slightly longer; maxillary palpal ratio about 4.5:4.0:3.5:1.0; clypeus relatively flat, lateral angle separated from eye margin by less than half minimum diameter of first flagellar segment, with median boss near apex but not usually carinate; supraclypeal area shiny, unshagreened, impunctate or punctures sparse and minute; lateral flattened areas of vertex with small punctures separated by one or less puncture widths, shiny. Mesoscutum with large, deep, round, variable-sized punctures, in posteromedian area separated

mostly by one puncture width or slightly more, surface often slightly dulled by reticular shagreening; mesepisterna moderately shiny, surface somewhat dulled by coarse, reticular shagreening. Metasomal tergum 1 with punctures of basal three-fifths small, shallow, separated mostly by one to one and one-half puncture widths, surface dulled by dense, reticulotransverse shagreening; terga 2 and 3 with interband zone punctures scarcely broader than base of hairs arising from them, separated mostly by two to three puncture widths or more, surface dulled by dense reticular shagreening, apical areas moderately shiny, impunctate.

Hair: Color as in *menuachus* except as follows: labrum and mandible often brown; anterior and lower lateral surfaces of mesepisterna dark brown; tergum 2 with interband zone hairs appressed to suberect, long, distal and basal pale bands confluent laterally and medially; tergum 3 with apical area usually as long as half width of distal pale band, with suberect, relatively simple, white or brown hairs; terga 5 and 6 without lateral pale tufts; sterna dark brown; legs as in *menuachus* but coxae dark brown, usually femora and trochanters dark brown at least below and occasionally entirely so; fore and middle distitarsi and basitarsi dark brown; hind basitarsi with inner surfaces and scopal hairs at apices of outer surfaces dark brown.

Male. Measurements and ratios: N, 20; length, 12-15 mm.; width, 3.5-5.5 mm.; wing length, $M = 4.36 \pm 0.212$ mm.; hooks in hamulus, $M = 15.10 \pm 0.176$; flagellar segment 2/segment 1, $M = 4.24 \pm 0.064$.

Structure and color: Integumental color as in *menuachus* except as follows: first flagellar segment usually dark brown or black, rarely red or yellow below; eyes brownish yellow to green; tegulae testaceous; wing veins red to reddish brown.

Structure as in *menuachus* except as follows: minimum length first flagellar segment equals one-fifth or slightly more of maximum length second segment, flagellum slightly crenulate near apex in lateral view (segments 9 and 10, and often 7 and 8, somewhat constricted below near base); maxillary palpal ratio about 3.0:2.7:2.3:1.0. Sculpturing as in female except as follows: tergum 1 with basal five-sixths with small round punctures mostly separated by one to two puncture widths, surface dulled by dense reticular shagreening, apical area beneath apical pale pubescent band with minute punctures and dulled at least basally; terga 2-4 with interband zone punctures minute, separated mostly by two to three puncture

widths, surface dulled by dense reticulotransverse shagreening, apical areas moderately shiny, impunctate; terga 5 and 6 similar but punctures more crowded.

Sterna 7 and 8 and genital capsule as in *menuachus* but sternum 7 with median plate with ventral hairs stouter (especially near base of plate).

Hair: Vestiture essentially as in *menuachus* but dull white rather than ochraceous and never bright ochraceous on dorsum of thorax or vertex of head.

Bionomics. This species is an oligolege of the composite genus *Chrysothamnus.* Females have been collected only from flowers of that genus (as far as the collection labels indicate), and males have been collected more often on *Chrysothamnus* flowers than on all other plants together. Isolated males, however, have been taken on *Solidago, Isocoma* and *Cleome* flowers and several were collected on sugar beets (whether on the inflorescence or on the harvested beets is not clear, but I suspect the latter).

Type Material. The male holotype of *semilupina* collected by Dr. A. Davidson at Los Angeles, California, is in the collection of the Natural History Museum of the University of Colorado at Boulder. The female holotype of *chrysothamni* collected at Embudo, New Mexico, September 16, 1897, by T. D. A. Cockerell on *Bigelovia* (= *Chrysothamnus*) sp. is in the collection of the U. S. National Museum (Type No. 40093).

Distribution. M. semilupina ranges from British Columbia and the Pacific Coast States east to Colorado and New Mexico (Fig. 13). It is most abundant in Oregon and California. This species has been collected from August 5 to October 29, but chiefly in September. In addition to the holotype, 22 females and 89 males have been examined from the localities listed below (including records reported in the literature).

Arizona: Tucson. California: Adelanto (8 miles S.), Mohave Desert; Anaheim; Deep Creek; Fort Tejon; La Jolla; Los Angeles; Los Angeles Co.; Morro Bay; Oro Grande; Riverside; San Diego Co.; Standish, Lassen Co.; Truckee (11 miles E. at Boca Dam); Victorville. Colorado: Alamosa; Great Sand Dunes National Monument. Nevada: Sparks, Washoe Co.; Sutcliffe, Washoe Co. New Mexico: Embudo; Abbotts Ranch, Rito de las Frijoles. Oregon: Arlington; Bend; Echo; Sisters (and 5 miles E.); Tumalo. Utah: Emery Co.; Iosepa; Juab Co.; Lehi; Park Valley. Washington: Hunts Junction; "Wash. Terr." Wyoming: Granger.

Canada. BRITISH COLUMBIA: Oliver; Vernon; Walhackin. ALBERTA: Magrath.

Flower Records. Chrysothamnus sp., *C. nauseosus, Cleome* sp., *Isocoma* sp., *Solidago occidentalis.*

Melissodes (Eumelissodes) ochraea, n. sp.

This species is closely related to both *menuachus* and to *semilupina.* The female is similar to that of *menuachus* in having tufts of pale hairs laterally on terga 5 and 6 and by having pale hairs on the lower lateral and anterior parts of the mesepisterna. However, the female of *ochraea* has the second flagellar segment distinctly shorter than broad, has a slightly more densely punctate mesoscutum than either *menuachus* or *semilupina,* and lacks suberect hairs in the apical area of tergum 3. The male of *ochraea* resembles that of *semilupina* in the form of the first flagellar segment and in having the dense, apical, pale pubescent band on the first tergum. It can be distinguished from *semilupina* by the more densely punctate mesoscutum.

The female of *ochraea* also resembles the female of *submenuacha* very closely. However, the males of these two species are quite distinct and the resemblance of the females does not, perhaps, indicate close relationship. The female of *ochraea* can be distinguished from that of *submenuacha* by the almost total lack of suberect hairs in the apical area of terga 2 and 3, by the dark brown hairs of terga 5 and 6 and of the sterna. The male of *ochraea* differs from that of *submenuacha* in the much longer first flagellar segment.

Female. Measurements and ratios: N, 20; length, 11-15 mm.; width, 3.5-5.0 mm.; wing length, $M = 4.33 \pm 0.171$ mm.; hooks in hamulus, $M = 16.60 \pm 0.222$; flagellar segment 1/segment 2, $M = 2.12 \pm 0.035$.

Structure and color: Integument black except as follows: apical half of mandible, often apical margin of clypeus, distitarsi, often basitarsi and occasionally rest of leg, and sterna rufescent; eyes gray; wing membranes colorless or slightly milky, veins reddish brown to black; tegulae piceous; tibial spurs yellow.

Clypeus flat, margin separated from eye by less than half minimum diameter of first flagellar segment, with median carina in apical half; maxillary palpal ratio about 4.5:2.5:3.0:1.0, (in one paratype from Whitewater, California, a distinct fifth segment equal in length to fourth is present); clypeus with round, shallow, coarse punctures separated mostly by less than half a puncture width, surface (and

bases of punctures) somewhat dulled by coarse, reticular shagreening; galeae above shiny, slightly dulled in apical half or less by reticular shagreening; vertex with lateral flattened areas with small punctures of irregular size separated mostly by half to two puncture widths, surface shiny. Thoracic sculpturing as in *menuachus* but mesoscutum with posteromedian area punctures separated mostly by less than one puncture width and often dulled by delicate reticular shagreening, scutellum shiny and punctures crowded, mesepisterna shiny, shagreening, if present, extremely delicate. Tergal punctation as in *semilupina*; terga 1-3 with apical areas impunctate, shiny, reticulotransverse shagreening extremely fine. Pygidial plate V-shaped, with apex more pointed than in *submenuacha*, *menuachus* or *semilupina*.

Hair: Head and thorax ochraceous, paler on clypeus, frons, genal areas, sides of thorax, and propodeum, often much brighter on vertex and dorsum of thorax (even being orangish here in some specimens but dark ochraceous in holotype). Metasomal pale pubescence and hairs pale ochraceous; tergal vestiture as in *menuachus* except as follows: tergum 3 with distal pale band separated from apical margin across entire tergum, apical area glabrous, without suberect hairs except occasionally a few at extreme base of area near pale band, medially apical area at least as long as pale band. Leg hairs as in *menuachus* except inner surfaces of hind basitarsi often reddish brown (as in holotype) and occasionally red.

Male. Measurements and ratios: N, 14; length, 12-14 mm.; width, 3-4 mm.; wing length, $M = 4.06 \pm 0.216$ mm.; hooks in hamulus, $M = 13.86 \pm 0.231$; flagellar segment 2/segment 1, (13) $M = 4.31 \pm 0.134$.

Structure and color: Integument black except as follows: clypeus and base of mandible yellow; labrum cream-colored except brown apical margin; flagellum yellow to red below (except first segment), reddish brown to black above; eyes gray to green; distitarsi and sterna rufescent; wing membranes colorless, veins red to reddish brown; tegulae testaceous (allotype) to piceous; apical areas of terga hyaline, colorless to slightly yellow.

Structure as in *menuachus* except as follows: minimum length of first flagellar segment equals one-fifth or more (more in allotype) of maximum length second segment; maxillary palpal ratio about 4.0:3.5:3.5:1.0, minute fifth segment sometimes present; clypeus flat. Sculpturing as in female except as follows: metasomal tergum 1 with basal five-sixths or more punctate, apical area beneath apical

pale band with minute punctures; terga 2, 3 and 4 with more distinct interband zone punctures separated mostly by about two puncture widths.

Sterna 7 and 8 and genital capsule as in *menuachus* but hairs on gonostylus shorter, sparser, never bifid or trifid at apex and hairs of ventral surface of median plate of sternum 7 sparse and weak.

Hair: Head and thorax pale ochraceous to white, often somewhat darker on vertex and dorsum of thorax (pale in allotype). Metasomal vestiture as in *menuachus* except as follows: tergum 1 with apical pale band of long, appressed, plumose hairs hiding surface across entire tergum (unless worn); terga 2-4 with apical areas without suberect hairs except one or two rows limited to base of apical area near pale pubescent bands. Legs white to pale ochraceous except inner surfaces of tarsi yellow.

Type Material. The holotype female and allotype male from Whitewater, Riverside Co., California, October 27, 1934, were collected by C. D. Michener on *Isocoma acradenia.* Nineteen female and nine male paratypes from California are as follows: Whitewater: 1 female with the holotype; 5 females and 1 male on *I. acradenia*, October 27, 1934, P. H. Timberlake; 3 females and 2 males, October 27, 1934, A. L. Melander; 2 females on *I. acradenia*, November 12, 1932, P. H. Timberlake; 1 female, September 8, 1949. Indio: 3 males, October 13, 1935, E. G. Linsley; 1 male on *I. acradenia*, October 15, 1947, P. H. Timberlake; 1 male on *I. acradenia* (2.8 miles S. E.), October 23, 1951, P. H. Timberlake. Morongo Valley: 1 male on *Gutierrezia* sp., September 26, 1944, P. H. Timberlake. Vallecito, San Diego Co.: 7 females, September 24, 1936, C. M. Dammus. The holotype and allotype are in the Snow Entomological Collection of the University of Kansas, Lawrence. Paratypes are in the collections of the University of Kansas, P. H. Timberlake of the Citrus Experiment Station, Riverside, California, the University of California at Berkeley, Harvard University (Museum of Comparative Zoology), and in the author's collection.

Distribution. Southern California and Arizona (Fig. 10). Since only 13 specimens are known in addition to the type material, the data for these are listed below in full.

ARIZONA: Madera Canyon, Santa Rita Mts.: 1 male, October 4, 1956, G. D. Butler and F. G. Werner. Rosemont, Pima Co.: 1 female on *Baccharis* sp., October 9, 1954, F. G. Werner. Sabino Basin, Santa Catalina Mts.: 1 male, September 28, C. H. T. Townsend. Safford: 2 females on yellow composite, September 24, 1956, G. D.

Butler; 2 females on yellow composite (30 miles S.), September 24, 1956. Tucson: 1 female, October 20, 1919; 1 male, October 1927, J. A. Downes; 1 female, October 8, 1937, R. H. Crandall; 1 female, September 29, 1939, A. S. Rosenberg; 1 female, November 10, 1939, A. S. Rosenberg.

Melissodes (Eumelissodes) bimatris, n. sp.

This species is highly variable in the color of the vestiture and is closely related to *semilupina* and *ochraea*. Females, because of their color variation, are difficult to separate from the latter two species, especially if they have much of the pubescence worn away. The female is like *semilupina* in having suberect hairs in the apical areas of terga 2 and 3, but the second flagellar segment is usually distinctly broader than long ventrally. The female also differs from *semilupina* females in the sculpturing of the interband zones of terga 2 and 3, as described below, and in the erect hairs in these zones. The female can be readily distinguished from that of *ochraea* by the punctation of the mesoscutum and the first metasomal tergum, and by the erect hairs of the interband zones of terga 2 and 3. The males are readily distinguished by lacking yellow maculae at the mandibular base, by the labrum being all or mostly black, and by the sparse mesoscutal punctures. The darkest females resemble *M. (Callimelissodes) nigracauda* from which they differ by the shiny galeae and pale scopal hairs.

Female. Measurements and ratios: N, 20; length, 11-15 mm.; width, 4.0-5.5 mm.; wing length, M = 4.10 ± 0.150 mm.; hooks in hamulus, M = 14.75 ± 0.298; flagellar segment 1/segment 2, M = 1.96 ± 0.022.

Structure and color: Integument black except as follows: apical half of mandible, often distitarsi, and flagellar segments 3-10 below rufescent; eyes gray; wing membrane colorless to slightly milky; veins dark reddish brown to black; tegulae piceous; tibial spurs colorless to pale yellow. Apex of tergum 1 narrowly hyaline.

Clypeus relatively flat, lateral angle separated from eye margin by half minimum diameter first flagellar segment or less, with median longitudinal carina usually present; second flagellar segment slightly broader at apex than median ventral length; maxillary palpal ratio about 3.0:2.7:2.3:1.0; galeae shiny, unshagreened above except perhaps delicately so in apical half or less. Sculpturing of head and thorax as in *ochraea* except posteromedian mesoscutal punctures separated mostly by more than one puncture width and often by two

or more puncture widths, surface unshagreened. Tergal sculpturing as in *menuachus* except as follows: tergum 1 with basal two-thirds or more (medially) punctate, punctures shallow, separated by one-half to one and one-half puncture widths and reaching apical margin at extreme sides, impunctate apical area not expanded basally at sides into impunctate lateral lobes; tergum 2 with interband zone punctures minute, separated by one to three puncture widths; terga 2 and 3 with apical areas with minute punctures at least basally near distal pale bands. Pygidial plate broadly V-shaped with well-rounded apex, usually less than eight-tenths as broad at base as median length.

Hair: Head pale ochraceous to entirely black, dark hairs appear first on labrum and mandibles, second on clypeus and vertex from which areas they spread over entire head in darker specimens. Thorax pale ochraceous to white laterally and posteriorly and dull ochraceous to somewhat rufescent above in palest specimens; in darkest specimens lateral and posterior surfaces, propodeum, tegulae, and anteriorly on mesoscutum dark brown to black, remainder of dorsum pale ochraceous to pale rufescent, posteromedian area of mesoscutum and median area of scutellum without dark hairs; intermediate specimens with entire dorsum, entire propodeum and upper lateral surfaces pale. Metasoma of palest specimen as in *ochraea* except as follows: interband zone of tergum 2 with hairs erect and without suberect or appressed plumose hairs; tergum 2 with distal pale band well separated from basal band except at extreme sides; tergum 4 with distal pale band narrow, medially narrower than basal area of dark hairs; terga 5 and 6 with little or no pale hairs laterally. Darkest specimens with metasomal vestiture entirely dark brown to black; pale hairs appear first at extreme base of tergum 2, second at base of tergum 1 and in distal pubescent band of tergum 2, third on tergum 3, and lastly on succeeding terga. Tergum 1 with long apical hairs of basal area appressed and reaching or overpassing margin across entire tergum whether these dark or pale (often worn away medially, however). Legs as in *ochraea* in pale specimens; in dark specimens dark brown to black except as follows: scopal hairs (except surrounding pygidial plate and at apex of basitarsus) ochraceous to yellow, inner surface hind tibiae ochraceous to yellow, hind femora often paler above, inner surface hind basitarsus dark brown to black.

Male. Measurements and ratios: N, 20; length, 10-14 mm.; width, 3.0-4.0 mm.; wing length, M = 3.88 ± 0.167 mm.; hooks in hamulus,

M = 13.30 ± 0.219; flagellar segment 2/segment 1, M = 4.68 ± 0.089.

Structure and color: Integument as in *menuachus* except as follows: base of mandible black; labrum entirely black (allotype) or with small mediobasal pale spot; clypeus yellow with apical margin usually piceous; first flagellar segment dark brown; eyes gray to green; wing veins dark reddish brown to black; tegulae piceous. Structure as in *menuachus* except as follows: minimum length first flagellar segment one-fifth or less (less in allotype) maximum length second segment, penultimate 3 or 4 segments slightly crenulate (as in *semilupina*); maxillary palpal segments in ratio of about 4.0:3.5: 3.5:1.0. Sculpturing as in female except as follows: metasomal tergum 1 with more than basal five-sixths (medially) punctate; terga 2 and 3 with punctures usually slightly coarser and more crowded.

Sterna 7 and 8 and genital capsule as in *M. menuachua* except gonocoxite without ventral hairs just below gonostylus.

Hair: Head and thorax white to pale ochraceous, often somewhat darker ochraceous on vertex of head and dorsum of thorax. Metasomal vestiture as in *ochraea* except distal pale bands of terga 2-4 (especially tergum 2) usually narrower than apical apubescent area; terga 2-4 with apical areas with abundant suberect pale hairs; tergum 2 with interband zone hairs erect; tergum 1 with distinct band of pale appressed pubescence obscuring apical margin across entire tergum. Two specimens (one from Santa Ana River, San Bernardino County and the other from Long Barn, Tuolumne County, California) with hairs and pubescence yellow-ochre to pale rufescent and brownish red in basal areas of terga 3 to 5. Legs as in *ochraea*.

Remarks. This species is very remarkable because of the marked dimorphism in color of the females. This is not reflected in the males. The females present two distinct color patterns in the vestiture. These two extremes are described above. There are intermediate specimens, but these are relatively few in number. Out of a total of 173 females, 96 were classified as the darkest form, 73 as the pale form, 7 as almost perfectly intermediate, 14 as intermediate but nearer the dark form, and 9 as intermediate but near the pale form.

It seems likely that a single pair of alleles, or a very few loci, are involved in the genetic background of this dimorphism. The intermediate types could be explained by microclimate affecting the rate of development and thus affecting melanism deposition during the prepupal or pupal stages of development. Significant in this respect

is the fact that there are so very few intermediate specimens and the majority of these are more like one or the other of the extremes in color than they are like the few almost exact intermediates. Furthermore, the dimorphism follows no apparent geographical pattern. Both forms of females and intermediates are available from such widely separated areas as Utah, Nevada, and northern and southern California. During preliminary studies, the author had segregated the females as two distinct species. There remains a possibility that this is the true situation. However, with the accumulation of additional specimens intermediate forms have become available. Furthermore, the two extreme forms, plus intermediates, have been collected in several instances at the same time, from the same flowers, and with the same males.

Bionomics. This species is apparently oligolectic on Compositae and, in particular, upon the genus *Chrysothamnus*, as is its close relative *M. semilupina.* Out of a total of 72 collections (93 females and 51 males) with floral data attached, 53 collections (80 females and 41 males) were made from some species of *Chrysothamnus*, whereas only 19 collections (13 females and 10 males) were obtained from other composites representing 11 genera.

Type Material. Holotype female (pale form) and two female paratypes (one an intermediate form) collected by E. G. Linsley on *Chrysothamnus nauseosus speciosus*, September 7, 1957, from 8 miles S. of Ravendale, Lassen Co., California. Allotype male from 15 miles S. of Ravendale was collected by B. J. Adelson on *Chrysothamnus nauseosus consimilis*, September 7, 1957. The holotype and allotype are in the collection of the University of California at Berkeley. Five male and twenty-seven female paratypes from California are as follows: LASSEN CO.: Depau: 2 females, October 11, 1952, E. I. Schlinger. Hallelujah Junction: 1 female on *Chrysothamnus nauseosus consimilis*, (2.5 miles S.), September 6, 1957, E. G. Linsley; 1 female on *C. n. consimilis*, (6 miles N.) B. J. Adelson. Janesville (1 mile N.): 1 female on *C. n. speciosus*, September 8, 1957, B. J. Adelson; 3 females on *C. n. speciosus*, September 8, 1957, E. G. Linsley. Litchfield: 2 males on *C. v. viscidiflorus*, September 8, 1957, E. G. Linsley. Madeline (8 miles N.): 1 female on *C. n. speciosus*, September 7, 1957, J. A. Chemsak. Standish (4 miles W.) 1 female on *C. v. viscidiflorus*, September 7, 1957, E. G. Linsley. MODOC CO.: Alturas (8 miles N.): 1 female and 1 male, September 7, 1957, J. A. Chemsak. Cedar Pass: 8 females and 1 male, October 11, 1952, E. I. Schlinger. Juniper Flat: 1 female, July 1938, J. J. DuBois.

Mason Creek Railroad Siding: 4 females, October 12, 1952, E. I. Schlinger. NEVADA CO.: Hobart Mills (7 miles N.): 1 female on *Chrysothamnus* sp., August 26, 1948, P. D. Hurd. Truckee (11 miles E. at Boca Dam): 1 female, September 15, 1957, E. G. Linsley. SIERRA CO.: Sierraville (3 miles N. W.): 1 female and 1 male on *Chrysothamnus* sp., September 9, 1957, E. G. Linsley. Twenty-nine male and four female paratypes from Washoe County, Nevada, are as follows: Purdy: 1 female on *Chrysothamnus* sp., September 6, 1957, E. G. Linsley; 1 female on *C. n. consimilis,* September 6, 1957, B. J. Adelson. Reno: 1 female and 1 male from 2 miles N., September 6, 1957, E. G. Linsley; 1 female from 7 miles N. on *C. n. consimilis,* September 6, 1957, J. A. Chemsak. Sparks: 1 male from 12 miles N. on *Chrysothamnus* sp., September 2, 1957, E. G. Linsley; 21 males from 17 miles N. on *C. n. consimilis,* September 2, 1957, E. G. Linsley. Sutcliffe: 2 males on *Chrysothamnus* sp., 4 males without floral data, September 2, 1957, E. G. Linsley. Paratypes are in the collections of the University of California at Berkeley and at Davis, R. R. Snelling, Turlock, California, the Snow Entomological Museum of the University of Kansas at Lawrence, and in the author's collection.

Distribution. M. bimatris ranges from British Columbia south to southern California and east to Colorado and New Mexico (one eastern Colorado male is dubiously identified as *bimatris,* although it is in very poor condition (Fig. 12). It has been collected from June to November 8, but mainly during September. In addition to the type material, 148 females and 73 males have been examined from the localities listed below.

Arizona: Black Mesa (near Kayenta); Pearce; Safford (30 miles S.); Tombstone (E. of); Yuma. California: Apple Valley, San Bernardino Co.; Barton Flatts; Caliente Mt. (2 miles N. E.), San Luis Obispo Co.; Carbon; Carmel; Deep Creek, Mojave Desert; Democrat Springs, Kern Co.; Gazelle; Helendale; Hesperia, S. Bernardino Co.; Imperial Co.; Lancaster (2 miles N.); Little Lake, Inyo Co.; Livermore (20 miles S. at Arroyo Mocho); Long Barn, Tuolumne Co.; Los Angeles Co.; McArthur; Morongo Valley; Murphys; Olancha (13 miles S.); Oro Grande; Paynes Creek, Tehama Co.; Riverside; Santa Ana River, S. Bernardino Co.; Seven Oaks; Sonora Pass, Mono Co.; South Fork Camp, S. Bernardino Mts.; Tesla; Turlock; Victorville, Vincent; Westgard Pass, Inyo Co.; Whitewater. Colorado: Berkeley; Cortez. Idaho: Bliss, Conant; Parma; Ridgedale. Nevada: Eureka; Walker Lake, Mineral Co. New Mexico:

McCartys, Valencia Co.; Mescalero. OREGON: Abert Lake; Algoma, Klamath Lake; Echo; Redmond. UTAH: Arches National Monument; Beryl; Blanding (19 miles W.); Dugway Proving Ground, Tooele Co.; East Promontory; Freemont Pass, Iron Co.; Lehi, Logan; Milford; Pine Valley Mts.; Promontory; Salt Lake; Torrey; Tridell. WASHINGTON: Brewster; Coulee City; Gardena; North Yakima; Pasco; Stratford. *Canada.* BRITISH COLUMBIA: Nicola; Oliver; Wallhackin. *Mexico.* SONORA: Agua Priete.

Flower Records. Artemesia sp., *Aster* sp., *Centromadia pungens, Chaematoris* sp., *Chrysothamnus* sp., *C. nauseosus, C. n. consimilis, C. n. gnaphalodes, C. n. mohavensis, C. n. occidentalis, C. n. speciosus, C. parryi, C. viridulus, C. viscidiflorus viscidiflorus, Ericameria palmeri, Eriogonum* sp., *Gutierrezia californica, G. lucida, G. sarothrae, Helianthus* sp., *Isocoma acradenia, Rhamnus californica, Senecio* sp.

Melissodes (Eumelissodes) cerussata, n. sp.

This species is known only from three females from San Bernardino County, California. These females resemble the females of *M. menuachus* in the shiny galeae, the long first flagellar segment, the dark hairs of the inner surfaces of the hind basitarsi, and in size, but differ in the generally white vestiture, the abundant, minute punctures in the apical area of tergum 3 and of tergum 2 (but less distinct in the latter). The female also resembles the palest female of *M. bimatris,* but differs from the latter in the punctate tergal apices and the pale lateral tufts of hair on terga 6 and 7.

Female. Measurements and ratios: N, 3; length, about 13 mm.; width, about 4.5 mm.; wing length, $M = 3.79 \pm 0.406$ mm.; hooks in hamulus, $M = 15.67 \pm 0.882$; flagellar segment 1/segment 2, $M = 188 \pm 0.058$.

Structure and color: Integumental color as in *menuachus* except as follows: eyes gray; tergum 1 with apical area translucent, red to yellow; flagellar segments 3 to 10 and apex of 2 yellow below. Structure and sculpture as in *menuachus* except as follows: clypeal punctures small, round, surface dulled by tessellation; supraclypeal area with few punctures medially, surface moderately shiny, tessellate; second flagellar segment slightly longer than broad; maxillary palpal ratio about 4.0:3.4:2.8:1.0; lateral areas vertex with small round punctures separated by half to one or slightly more puncture widths, surface shiny but somewhat shagreened; mesoscutum with small impunctate posteromedial area, surface with

fine reticular shagreening scarcely dulled; metasomal tergum 1 with basal three-fourths with round punctures separated mostly by half to one puncture width, apical area impunctate, without anterolateral impunctate lobes; tergum 2 with basal area punctures separated mostly by half a puncture width or less, interband zone punctures small, separated mostly by one puncture width, surface dulled, apical area with minute but distinct punctures separated mostly by two to three puncture widths, surface moderately shiny; tergum 3 similar to 2 but apical area punctures more distinct and more crowded.

Hair: Head and thorax white except lower surfaces mesepisterna pale brown. Vestiture of metasomal terga as in *menuachus* except as follows: tergum 1 with basal area hairs white, apical area glabrous, basal hairs often reach apex of tergum medially; tergum 2 with all hairs and pubescence white, apical area hairs abundant, subappressed to suberect, white; tergum 3 like 2 but basal tomentum brown, apical area hairs more abundant, distal pale band reaches apex at extreme sides; tergum 4 like 3 but lacking apical area; terga 5 and 6 dark brown with white lateral tufts. Legs white except basitibial plates orange, fore tarsi and inner surfaces middle and hind basitarsi dark brown, and inner surfaces hind tibiae yellow.

Type Material. The holotype female from six miles west of Ludlow, San Bernardino Co., California, was collected October 17, 1951, on *Geraea* sp., by E. G. Linsley. Two female paratypes were collected at the same time and place on the same flower by P. D. Hurd and Ray F. Smith, respectively (see Fig. 10 for distribution). The holotype and one paratype are in the collection of the University of California at Berkeley. The second paratype is in the author's collection.

Melissodes (Eumelissodes) relucens, n. sp.

This species is closely related to *menuachus* and to *ochraea*. It is similar to *menuachus* in the color of the vestiture except that the females usually have paler hairs on the inner surfaces of the hind basitarsi. The females can be separated from those of *menuachus* and *ochraea* by the coarser punctation of the mesoscutum, the first tergum, and the interband and basal areas of the second tergum. The female has the second flagellar segment about as long as broad. The male of *relucens* has a short first flagellar segment and a long penultimate segment as in *menuachus*. The punctation of the male is similar to that of the female, but is much coarser

at the base of the second tergum and on the sterna. In addition, the male is distinctive in having an extremely broad pygidial plate.

Female. Measurements and ratios: N, 2; length, about 13 mm.; width, about 4.5 mm.; wing length, 3.74-3.79 mm.; hooks in hamulus, 13; flagellar segment 1/segment 2, 1.82-1.91.

Structure and color: Integument black except as follows: apical half of mandible, lower surfaces of flagellar segments except first, distitarsi, and sterna rufescent; eyes green; wing membrane colorless, veins dark brown to black; tegulae piceous; tibial spurs yellow to pale rufescent. Structure and sculpturing as in *menuachus* except as follows: clypeal punctures coarser, irregular in size, crowded, with subapical median shiny boss, surface shiny, unshagreened; supraclypeal area shiny; galeae above shiny, unshagreened; lateral areas of vertex with minute, sparse punctures, shiny; maxillary palpal ratio about 8:7:5:1. Mesoscutal punctures large, deep, round, crowded, posteromedially largest and separated mostly by half a puncture width or slightly more, surface with fine reticular shagreening but not or scarcely dulled; scutellum similar but punctures smaller; mesepisternal punctures small, round, deep, separated mostly by less than half a puncture width, mostly less in diameter than posteromedian mesoscutal punctures, surface shiny; propodeum with dorsal surface coarsely reticulorugose basally, with irregular punctures apically except medially, posterior surface punctate except upper inverted triangular area, lateral surfaces coarsely punctate, surfaces moderately shiny, upper triangle of posterior surfaces with fine, reticular shagreening slightly dulling surface. Tergum 1 with basal three-fifths medially with small round deep punctures separated mostly by half to one puncture width, punctures to apex laterally; terga 1-3 with apical areas impunctate, surfaces shiny with extremely fine reticulotransverse shagreening; tergum 2 with basal area with deep, small, round punctures separated mostly by half a puncture width or less, interband zone with small, irregular-sized and spaced punctures separated mostly by one puncture width; pygidial plate V-shaped with relatively straight sides and acute apex.

Hair: Color of vestiture as in *menuachus* except as follows: dorsum of thorax bright ochraceous to yellow and hairs short and appressed; metasomal pale pubescent bands white, that on tergum 2 not reaching apical margin and of almost equal width across tergum (not notched posteriorly as in *ochraea*), that on tergum

3 reaching apex at extreme sides; terga 2 and 3 with interband zone hairs white, short, appressed (unlike *bimatris*); sterna reddish brown except white laterally; legs white except brown on fore tarsi and on basitibial plate, basitarsi with inner surfaces red to reddish brown.

Male. Measurements and ratios: N, 1; length, about 11 mm.; width, about 3.5 mm.; wing length, 3.63 mm.; hooks in hamulus, 12; flagellar segment 2/segment 1, 6.36.

Structure and color: Integument black except as follows: clypeus yellow except brown apical margin; labrum with minute pale mediobasal spot; base of mandible with minute yellow spot; eyes gray; lower surface of flagellum yellow, upper dark reddish brown; apical half of mandible, distitarsi and sterna rufescent; wing membrane colorless, veins dark reddish brown; tegulae piceous; tibial spurs reddish yellow; tergal apices hyaline, yellow; pygidial plate red.

Structure as in *menuachus* except as follows: minimum length first flagellar segment one-sixth of maximum length second segment or slightly less, penultimate segment almost four times as long as broad; maxillary palpal ratio about 14:12:7:1. Sculpturing as in female except as follows: tergum 1 with basal four-fifths punctate; tergum 2 with basal area punctures coarser than in female (in diameter almost equal to tergum 1 punctures); terga 2 and 3 with interband zone punctures coarser and more abundant; sternal punctures large and crowded. Pygidial plate broader than median length, deeply notched in apical third so that apical portion less than half as broad as broadest width near base.

Terminalia much as in *agilis* but median plates of sternum 7 with sparse hairs, gonostyli with hairs sparse, inner surfaces gonocoxites with blunt spicules sparse, and sternum 8 with apical hairs sparse and short.

Hair: Color and form of vestiture as in *menuachus* with same exceptions as in female.

Type Material. Holotype female and allotype male from Dugout Wells, Big Bend National Park, Texas, collected on August 25, 1954, by R. M. Bohart are in the collection of the University of California at Davis. One female paratype from El Paso, Texas, collected by H. V. Daly, September 13, 1950, on *Isocoma heterophylla* is in the collection of the Snow Entomological Museum of the University of Kansas at Lawrence (Fig. 15).

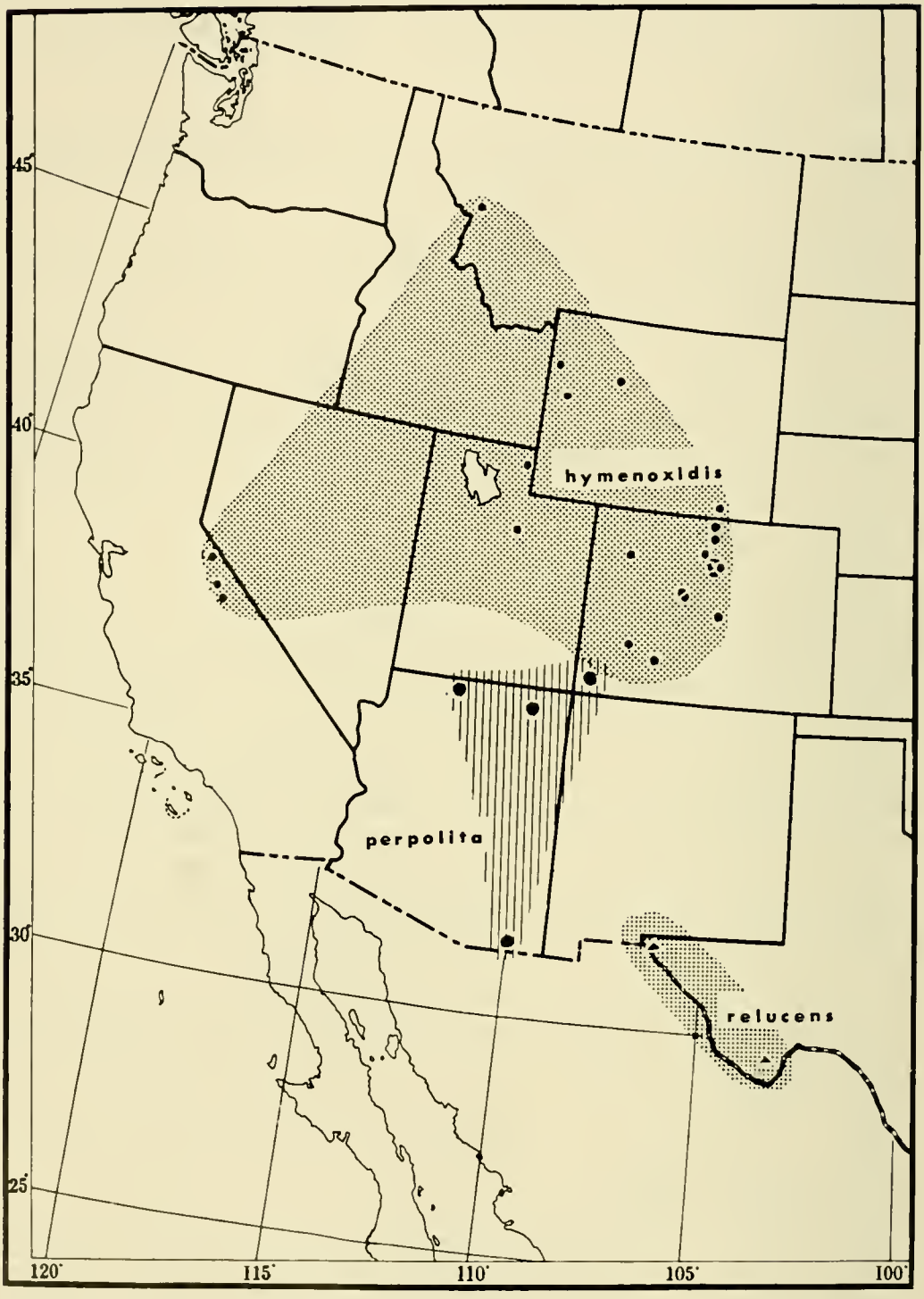


FIG. 15. Map showing the known distributions of *M. (Eumelissodes) hymenoxidis* Cockerell, *M. (E.) perpolita* LaBerge, and *M. (E.) relucens* LaBerge.

Melissodes (Eumelissodes) bicolorata, n. sp.

This species seems to be most closely related to *M. bimatris* and the females of *bicolorata* closely resemble the darker females of *bimatris*. However, the females of *bicolorata* have fuscous scopal hairs, unlike those of *bimatris*. In the dark scopal hairs and general vestitural color, *bicolorata* is almost identical with *M. (Callimelissodes) nigracauda* from which it differs by the subgeneric characteristics and by having shiny, unshagreened galeae. The male of *bicolorata* is a medium sized, pale bee with pale wing veins not unlike *M. agilis* from which it differs by the dark labrum and mandibular bases. The male closely resembles that of *bimatris* from which it can be distinguished by the lack of a distinct apical pale pubescent band obscuring the apex of the first tergum, by the pale wing veins, and by the flagellum not being crenulate (as it is in both *bimatris* and *semilupina*).

Female. Measurements and ratios: N, 20; length 10-13 mm.; width, 3.5-4.5 mm.; wing length, $M = 3.55 \pm 0.096$ mm.; hooks in hamulus, $M = 14.50 \pm 0.212$; flagellar segment 1/segment 2, $M = 1.96 \pm 0.024$.

Structure and color: Integument black except as follows: apical half of mandible, usually distitarsus and lower surfaces of flagellar segments 3-10 rufescent; eyes dark gray to greenish gray; wing membranes slightly milky, veins reddish brown to red; tegulae piceous; tibial spurs yellow; apex of tergum 1 piceous.

Structure and sculpturing as in *bimatris* except as follows: maxillary palpal ratio about 4.0:3.0:3.5:1.0; tergum 1 with basal three-fifths or less medially punctate, punctures not extending to apex laterally and impunctate apical area extending anterolaterally as indistinct lobes; tergum 2 with interband zone punctures minute and sparse; terga 2 and 3 with apical areas with punctures at bases of hairs minute and sparse but distinct and almost reaching apex of tergum at least laterally on tergum 2 and across entire tergum 3; pygidial plate broadly V-shaped with apex rounded, usually more than eight-tenths as broad at base as median length.

Hair: Head dark brown except long hairs of vertex and on face above and surrounding antennal fossae often pale ochraceous. Thorax above, including dorsal and posterior surfaces of propodeum and often mesepisterna and metepisterna just below wing bases, pale ochraceous to slightly ferrugineous (fox-red), laterally and ventrally dark brown to black. Metasoma dark brown to black except as follows: tergum 1 with basal half to three-fifths of dorsal surface pale

ochraceous (holotype) to slightly rufescent and tergum 2 with basal zone hairs often ochraceous to pale brown (dark in holotype). Legs dark brown except as follows: median scopal hairs of tibiae and occasionally near base of basitarsi usually paler brown to ochraceous.

Male. Measurements and ratios: N, 7; length, about 11 mm.; width, about 3.5 mm.; wing length, M = 3.53 ± 0.211 mm.; hooks in hamulus, M = 12.86 ± 0.509; flagellar segment 2/segment 1, M = 7.30 ± 0.351.

Structure and color: Integument as in *bimatris* except as follows: labrum without mediobasal pale spot; first flagellar segment yellow to red below; eyes greenish gray; wing membranes slightly milky, veins yellow to reddish yellow; tergal apices hyaline, colorless.

Structure as in *bimatris* except as follows: minimum length of first flagellar segment equals about one-sixth maximum length of second segment, penultimate 3 or 4 segments not crenulate; maxillary palpal segments in ratio of about 4:3:3:1. Sculpturing as in female except as follows: tergum 1 with basal four-fifths punctate; terga 2 and 3 with interband zone punctures slightly larger and more crowded, and with apical area punctures indistinct and sparse; tergum 4 similar to tergum 3. Pygidial plate broad but more as in *bimatris* than as in *relucens,* width at base subequal to median length and usually slightly less.

Sterna 7 and 8 and genital capsule as in *M. menuachus* except as follows: gonostyli gently curved in or straight, scarcely capitate, with hairs near base sparse; gonocoxite with a few extremely short hairs at apex just below gonostylus on ventral surface; spatha with well-marked, apicomedian, shallow notch; sternum 7 with median plate with apical margin transverse; sternum 8 with ventral tubercle bidentate, with abundant apical hairs.

Hair: Vestiture white to extremely pale ochraceous (usually pale ochraceous only on upper surface of thorax). Metasomal vestiture as in *bimatris* except as follows: tergum 1 without distinct pale pubescent band obscuring apical margin except at extreme sides and these in width less than a third width of tergum; terga 2-4 with apical area hairs suberect and less abundant; tergum 2 with interband zone hairs suberect.

Type Material. The holotype female, allotype male and 23 female paratypes were collected by C. D. Michener at Dayton, Nevada, July 1, 1950 on *Penstemon palmeri.* Two female paratypes from Nevada are as follows: 1 female on June 20 and 1 female on June 29, 1927, at Nixon by E. P. Van Duzee. In addition, 17 fe-

male and 5 male paratypes from California are as follows: Hallelujah Junction, Lassen County: 1 male, July 7, 1949, P. D. Hurd; 1 male, July 13, 1949, P. D. Hurd; 1 male, July 13, 1949, E. I. Schlinger; 2 females and 2 males, July 13, 1949, F. Morishita; 11 females, July 13, 1949, on *Chrysothamnus* sp., P. D. Hurd; 3 females, August 9, 1949, on *Chrysothamnus* sp., J. W. MacSwain. Murphys, Calaveras County: 1 female, September 8-19, 1937, F. E. Blaisdell. The holotype and allotype are in the Snow Entomological Collection of the University of Kansas, Lawrence. Paratypes are in the collections of the Snow Entomological Collection, the University of California at Berkeley, the University of California at Davis, the California Academy of Sciences at San Francisco, P. H. Timberlake at the Citrus Experiment Station, Riverside, California, the U. S. National Museum, Washington, D. C. and in the author's collection.

Distribution. Northern California, Nevada and Utah (Fig. 10). In addition to the 52 specimens from California and Nevada listed above as type material, 3 specimens have been examined from Utah as follows: Leota: 3 females, July 17, 1952, on sweet clover (*Melilotus* sp.), G. F. Knowlton and G. E. Bohart.

Melissodes (Eumelissodes) perpolita, n. sp.

This is a small coarsely punctate species similar to and related to *M. relucens*. The female of *perpolita* differs from that of *relucens* by the brown scutellar and mesoscutal hairs, the interband zone of tergum 2 being almost bare but with some brown hairs, the punctation of tergum 2 as described below, the longer apical areas of terga 2 and 3 and the presence of a small median glabrous apical area on tergum 4. The male of *perpolita* can be told from that of *relucens* by the slightly narrower pygidial plate and the less hairy and less punctate (although more coarsely so) interband zone of tergum 2. The allotype is the only known male of *perpolita* and, since it was not collected with any of the females, the association of the two sexes is tentative.

Female. Measurements and ratios: N, 4; length, about 10 mm.; width, about 3.5 mm.; wing length, M = 3.12 ± 0.225 mm.; hooks in hamulus, M = 12.00 ± 0.435; flagellar segment 1/segment 2, M = 1.84 ± 0.034.

Structure and color: Integumental color as in *relucens* except as follows: second flagellar segment dark below; eyes bluish gray (holotype) to gray; tegulae rufescent. Structure and sculpture as

in *menuachus* except as follows: clypeal punctures large, separated mostly by less than half a puncture width, surface unshagreened, apicomedian carina weak; supraclypeal area shiny; galeae shiny, unshagreened; lateral areas of vertex with punctures large, irregular, separated mostly by half to one puncture width; maxillary palpal ratio about 2.7:1.7:1.5:1.0; mesoscutal punctures very large, posteromedially larger than mesepisternal punctures and separated by half to two puncture widths (scattered irregularly), surface shiny; scutellar punctures slightly smaller, crowded; metasomal tergum 1 with basal two-thirds with round shallow punctures about same size as scutellar and separated mostly by half a puncture width, surface reticularly shagreened but shiny, apical area impunctate, finely shagreened, shiny, with anterolateral lobes separated from rest of apical area by an uneven double row of coarse punctures; tergum 2 with basal area punctures small, separated mostly by half to one puncture width, surface somewhat dulled by reticular shagreening, interband zone punctures irregular in size and distribution, largest as large as mesoscutal punctures, smallest minute, with conspicuous blank spaces between punctures, surface shiny with fine reticulotransverse shagreening, apical area impunctate, shiny, longer medially than distal pale band; tergum 3 similar to 2 but apical area shorter; tergum 4 similar to 3 but apical area reduced to small median triangle; pygidial plate V-shaped, apex acute.

Hair: Head white with brown on vertex. Thorax white with scutellum brown fringed with white and mesoscutum with posteromedian brown patch about one and one-half times size of scutellar dark area; tegulae without brown. Tergal vestiture as in *relucens* except as follows: tergum 2 with distal pale band slightly shorter than apical area medially, interband zone with short, simple subappressed to suberect hairs, usually at least partly brown and sparser than in *relucens*; tergum 3 similar but interband zone narrower and basal tomentum dark brown; tergum 4 with distal pale band interrupted apicomedially by triangular apubescent area; hind basitarsi with inner surfaces yellow to dark red; scopae white.

Male. Measurements and ratios: N, 1; length, about 11 mm.; width, about 3 mm.; wing length, 3.18 mm.; hooks in hamulus, 12; flagellar segment 2/segment 1, 5.07.

Structure and color: Integumental color as in *relucens* except as follows: labrum and mandibles black; eyes yellowish gray; first flagellar segment slightly less than one-sixth maximum length second segment, penultimate segment one-third as wide as long or slightly

less; maxillary palpal ratio about 3.0:2.5:2.5:1.0; pygidial plate longer than broad, apicolateral notches deep so that apical part half median width. Sculpture as in female except as follows: clypeal punctures smaller; terga 2 and 3 with interband zones with large punctures more abundant and more crowded; terga 4 and 5 similar to 3 but apical areas shorter.

Hair: Head and thorax white. Metasomal vestiture as in *relucens* except as follows: tergum 1 with apical area exposed; terga 2 and 3 with interband zones with hair less abundant. Legs white except inner surfaces hind basitarsi yellow.

Type Material. The holotype female from Black Mesa (near Kayenta), Arizona, was collected by Isabel McCracken, September 11, 1936, on *Chaemataxis* sp. The allotype male from Bisbee (10 miles N. W.), Arizona, was collected by T. Cohn, P. Boone and M. Cazier, September 7, 1950. Two paratype females from Kaibab Forest, Utah, (this is probably mislabelled "Utah" and should be Arizona), were collected by I. McCracken, September 21, 1938, on *Aster* sp. One paratype female from Cortez, Colorado, was collected by I. McCracken, September 13, 1938, on *Grindelia* sp. The holotype and one paratype are in the collection of the California Academy of Sciences, San Francisco. The allotype is in the American Museum of Natural History, New York City. Paratypes are in the collection of the Snow Entomological Museum of the University of Kansas, Lawrence and in the author's collection (Fig. 15).

Melissodes (Eumelissodes) fasciatella, n. sp.

M. fasciatella is a small distinctive bee from Arizona known only in the female sex. It is not closely related to any of the foregoing species but bears some resemblance in the tergal banding and punctation to *M. perpolita* so is treated here. *M. fasciatella* is distinctive in that the pale distal band of tergum 2 is reduced to two short lateral fasciae, each about one-third of the tergum in width and tapering sharply mesad, thus forming two short oblique fasciae. The extensive apical area of tergum 2 is impunctate and shiny. The galeae are shiny and hairs of the inner surfaces of the hind basitarsi are dark reddish brown.

Female. Measurements and ratios: N, 20; length, 9-10 mm.; width, 3.0-3.5 mm.; wing length, M = 2.71 ± 0.067 mm.; hooks in hamulus, M = 10.85 ± 0.150; flagellar segment 1/segment 2, M = 1.97 ± 0.238.

Structure and color: Integument black except as follows: mandi-

bles and distitarsi rufescent; flagellar segments 3-10 red below; eyes bluish to greenish gray; wing membranes colorless to milky, veins dark reddish brown; tegulae piceous; tibial spurs yellow; tergal apices often slightly rufescent, tergum 1 narrowly hyaline apically.

Structure and sculpture as in *perpolita* except as follows: lateral areas vertex with minute punctures separated by two to four puncture widths, surface shiny; maxillary palpal ratio about 2.0:1.7: 1.7:1.0; mesoscutal punctures large but not larger than mesepisternal, small posteromedial area usually impunctate, elsewhere punctures separated mostly by half to one puncture width, surface shiny, often (not in holotype) with fine reticular shagreening; mesepisternal punctures large, deep, separated by less than half a puncture width, surface shiny; metasomal tergum 1 with basal half or slightly more with large round punctures, not very shallow, separated mostly by half a puncture width or slightly more, surface reticulotransversely shagreened but shiny, apical area impunctate, shiny; tergum 2 with basal area punctures large, slightly less in diameter than those of base of tergum 1, separated mostly by half a puncture width, interband zone punctures smaller to slightly larger than those of basal area, separated by half a puncture width laterally to one or two puncture widths in median third, apical area impunctate, highly shiny; tergum 3 similar to 2 but apical area shorter and interband zone punctures small and denser; tergum 4 like 3 but lacking apical area; pygidial plate V-shaped, apex rounded, longer than broad.

Hair: Head white to pale ochraceous on vertex, vertex with few or no brown hairs. Thorax white laterally; scutellum dark brown fringed with pale ochraceous; mesoscutum pale ochraceous with large posteromedian dark brown patch usually twice size of scutellar dark area or larger; tegulae without brown; mesoscutal hairs short, blunt-tipped and usually decumbent except peripherally. Metasomal tergum 1 white to pale ochraceous basally and to apical margin at extreme sides, glabrous apicomedially; tergum 2 white basally; distal pale band in form of two lateral fasciae, each one-third or less width of tergum and sharply tapered towards middle of tergum to form short, oblique, lateral fasciae, interband zone with sparse, appressed to subappressed, pale ochraceous pubescence and bristle-like hairs, apical area glabrous; tergum 3 similar to 2 but basal tomentum brown, distal pale band not interrupted medially (although posterior margin slants forward to an obtuse point medially), and apical area shorter; tergum 4 like 3 but distal pale band reaches apical margin across entire tergum; terga 5 and 6 dark brown with

lateral white tufts at least on 5; sterna brown medially to white laterally. Legs white except as follows: fore tarsi, outer-apical surfaces fore and middle tibiae, and basitibial plates brown; inner surfaces hind basitarsi dark reddish brown to dark brown.

Type Material. The holotype female and one female paratype from Todd's Lodge, Oak Creek Canyon, Arizona, was collected on September 7, 1948, by Grace H. and John L. Sperry. The Sperrys also collected one female paratype at Todd's Lodge on September 29, 1948. In addition, 32 female paratypes from Arizona are as follows: Dos Cabezas (16 miles S.): 1 female, September 8, 1950, T. Cohn, P. Boone and M. Cazier. East Verde River: 6 females collected at 4,500 feet altitude. Madera Canyon, Santa Rita Mts.: 1 female on *Aplopappus gracile*, September 23, 1956, F. G. Werner. Onion Saddle (9 miles W.), Chiricahua Mts.: 2 females, September 10, 1954, J. C. Hall; 5 females on *A. gracilis*, September 10, 1954,

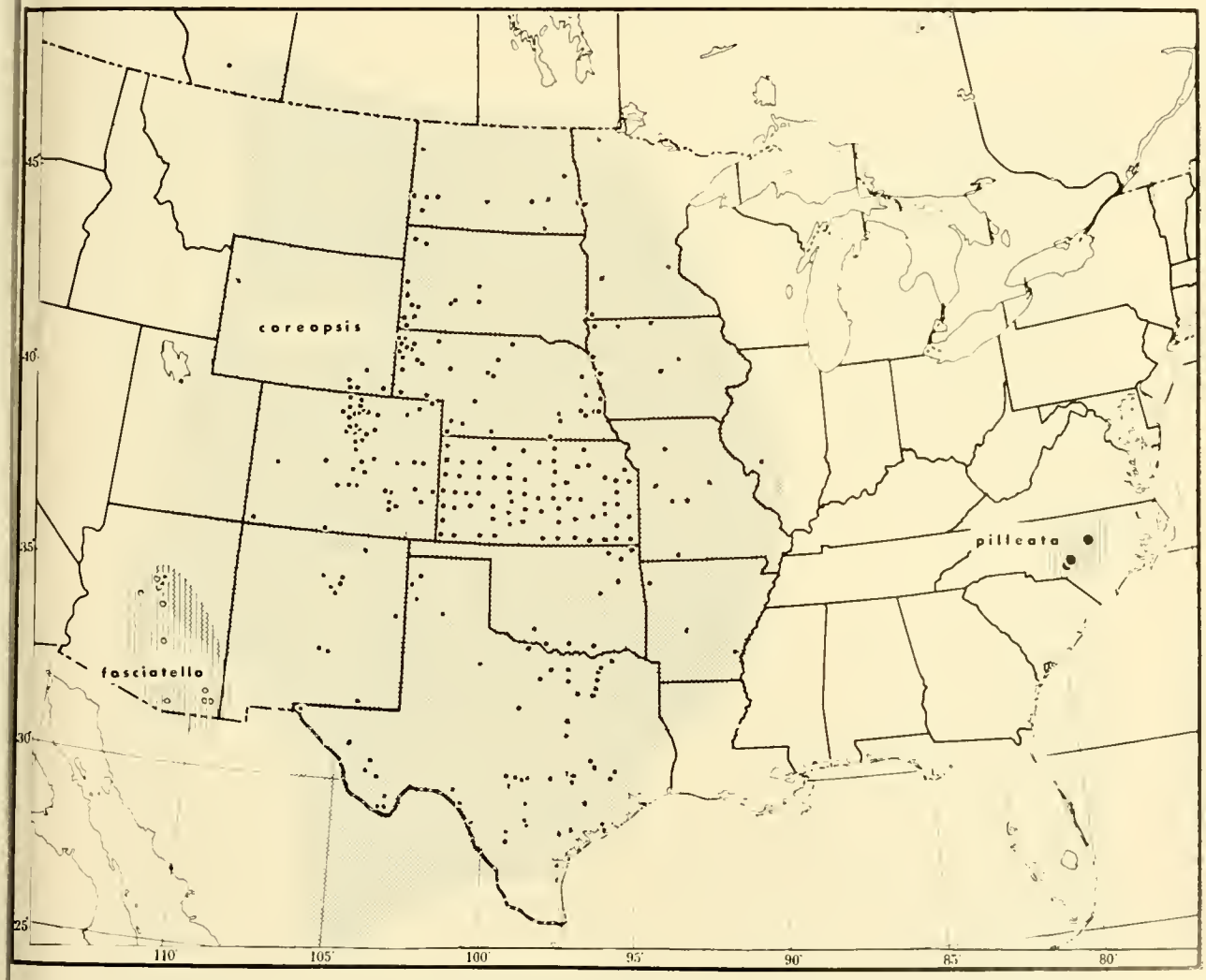


FIG. 16. Map showing the known distributions of *M. (Eumelissodes) fasciatella* LaBerge, *M. (E.) coreopsis* Robertson, and *M. (E.) pilleata* LaBerge.

P. H. Timberlake. Prescott: 2 females on *A. gracilis*, September 17, 1953, P. H. Timberlake. Price (2.9 miles N.): 3 females on *Erigeron* sp., 3 females on *A. gracilis*, September 17, 1953, P. H. Timberlake. Sedona: 2 females, September 14, 1955, G. D. Butler; 1 female on *Viguiera* sp. (10 miles N.), September 13, 1955, G. D. Butler. Seligman: 1 female on *Gutierrezia* sp., August 29, 1931, P. H. Timberlake. Southwest Research Station (5 miles W. of Portal): 2 females, September 8, 1955, W. Gertsch and E. Ordway. S. Arizona: 3 females, August 1902, F. H. Snow. The holotype is in the collection of the Snow Entomological Museum of the University of Kansas, Lawrence. Paratypes are in the collections of the Snow Entomological Museum, P. H. Timberlake, Riverside, California, The American Museum of Natural History, New York City, the U. S. National Museum, Washington, D. C., the University of Arizona, Tucson, the University of California at Davis, and in the author's collection (Fig. 16).

Melissodes (Eumelissodes) coreopsis Robertson

Melissodes coreopsis Robertson, 1905, Trans. Amer. Ent. Soc., vol. 31, p. 368; 1914, Ent. News, vol. 25, p. 69; 1926, Ecology, vol. 7, p. 379; 1928, Flowers and Insects, p. 8.

Melissodes agilis semiagilis Cockerell, 1906, Ann. Mag. Nat. Hist., ser. 7, vol. 17, p. 364 (new synonymy); 1907, Univ. Colo. Studies, 4:225; 1014, Canadian Ent., 46:413; 1919, Canadian Ent., 51:27; 1928, Univ. Colo. Studies, 16:114.

Melissodes confusiformis Cockerell, 1906, Ann. Mag. Nat. Hist., ser. 7, vol. 17, p. 366 (new synonymy); 1907, Univ. Colorado Studies, vol. 4, p. 255; 1910, Psyche, vol. 17, p. 246; 1914, Canadian Ent., vol. 46, p. 409; 1919, Canadian Ent., vol. 51, p. 272; 1923, Ent. News, vol. 34, p. 47; Bohart, Knowlton and Bailey, 1950, Utah St. Agric. Coll., Mimeo. Ser. No. 371, p. 5.

Melissodes helianthophila Cockerell, 1914, Ann. Mag. Nat. Hist., ser. 8, vol. 14, p. 361 (new synonymy).

Melissodes confusa, Robertson (*nec* Cresson, 1878), 1894, Trans. Acad. Sci. St. Louis, vol. 6, pp. 458-460, 468, 471, 474, 475; 1896, Trans. Acad. Sci. St. Louis, vol. 7, pp. 175, 176, 178; 1897, Trans. Acad. Sci. St. Louis, vol. 7, p. 355.

Melissodes coreopsis is the most common species of *Eumelissodes* of the Great Plains except perhaps *M. agilis*. It is a medium-sized bee, the female of which has black and white metasomal bands, a large black dorsal thoracic patch, pale scopal hairs with dark hairs on the inner surfaces of the hind basitarsi, and short subappressed dark hairs in the apical areas of terga 2 and 3. It is not closely related to any of the foregoing species but is most similar to *M. rustica* from which it differs by the paler thoracic and head hairs of both sexes, the less shiny terga of both sexes, the paler scopal hairs of the female, and the hyaline tergal apices and shorter first flagellar segment of the male. A relatively complete description

is given below after which subsequently described and related species are patterned.

Female. Measurements and ratios: N, 20; length, 9-14 mm.; width, 3.0-4.5 mm.; wing length, M = 3.38 ± 0.196 mm.; hooks in hamulus, M = 12.70 ± 0.206; flagellar segment 1/segment 2, M = 1.76 ± 0.024.

Structure and color: Integument black except as follows: apical half of mandibles and distitarsi (often basitarsi and tibiae as well) rufescent; lower surfaces of flagellar segments 3-10 and often apex of second segment yellow to red; eyes blue to bluish gray or dark gray; wing membranes hyaline, colorless or slightly milky, veins dark brown to black; tegulae piceous, occasionally slightly testaceous; tibial spurs white to yellow; tergum 1 usually rufescent in apical third or half and with extremely narrow apical margin hyaline and colorless or yellow.

Clypeus flat, oculoclypeal distance half minimum width of first flagellar segment or less, with punctures relatively regular, deep, round, separated mostly by half a puncture width or less, surface shiny, with irregular cross-striations especially near base; supraclypeal area with punctures sparse or absent medially, usually slightly dulled by fine reticluar shagreening; vertex with flattened lateral areas with small round punctures separated by one to two or more puncture widths, surface usually shiny; galeae above shiny, unshagreened except near tips; maxillary palpal ratio about 9:6:5:1, last segment often almost obliterated. Mesoscutal punctures large, round, deep, posteromedially larger and separated by one to three puncture widths, anteriorly and laterally smaller and separated by half to one puncture width or less; scutellar punctures smaller, medially separated mostly by one to two puncture widths; mesepisterna with lateral surface punctures as large or larger than posteromedian mesoscutal punctures, separated mostly by less than half a puncture width; surfaces of mesoscutum and scutellum usually shiny, often slightly dulled by delicate reticular shagreening; surfaces of mesepisterna usually unshagreened; propodeum with dorsal surface reticulorugose, coarser near base, posterior surface with abundant shallow punctures except in upper inverted triangular area, lateral surfaces densely punctate, surfaces everywhere dulled by fine, dense tessellation. Metasomal tergum 1 with basal half to three-fifths with small shallow punctures separated mostly by half a puncture width, apical impunctate area extended basally on each side to form indistinct anterolateral lobes, surface dulled

by dense reticulotransverse shagreening; tergum 2 with basal area punctures round, deep, separated by half to one puncture width, larger apically, surface shiny and unshagreened, interband zone punctures larger and shallower, separated by half to one puncture width laterally and mostly by one puncture width medially, surface dulled by dense reticulotransverse shagreening, apical area impunctate or with minute, widely separated punctures, surface dulled by dense shagreening; tergum 3 similar to 2 but punctures of interband zone smaller and more crowded and apical area with minute punctures somewhat more abundant. Pygidial plate broadly V-shaped with rounded apex, longer than breadth at base.

Hair: Head white to pale ochraceous with long brown hairs on vertex. Thorax white to pale ochraceous except scutellum dark brown with pale fringe and mesoscutum with posteromedian dark patch as large and usually larger than scutellar dark area; tegulae usually with brown hairs posteromedially. Metasomal tergum 1 with basal area white to pale ochraceous, apical area glabrous; tergum 2 with basal tomentum white and connected laterally by white pubescence to distal pale band, distal band white, laterally longer than apical area, narrowly interrupted medially, interband zone hairs subappressed to suberect, all or mostly dark brown, apical area with short, subappressed, relatively simple, brown to black hairs usually present except near apex; tergum 3 as in 2 but basal tomentum brown, distal pale band broader and usually uninterrupted medially, apical area narrower (distal pale band may reach apex at extreme sides), and with more abundant simple, subappressed, dark hairs in apical area; tergum 4 with apical pubescent band broad, white, uninterrupted posteromedially; terga 5 and 6 dark brown with pale lateral tufts; sterna brown or reddish brown medially to white laterally. Legs pale ochraceous to white except as follows: distitarsi yellow to reddish brown; fore basitarsi, inner surface middle and hind basitarsi, on and surrounding pygidial plate and often outer surfaces of apices of fore and middle tibiae reddish brown to dark brown; inner surfaces hind tibiae yellow.

Male. Measurements and ratios: N, 20; length, 8-12 mm.; width, 2.5-4.0 mm.; wing length, $M = 3.40 \pm 0.126$ mm.; hooks in hamulus, $M = 12.10 \pm 0.143$; flagellar segment 2/segment 1, $M = 8.71 \pm 0.204$.

Structure and color: Integument black except as follows: clypeus yellow except apical margin testaceous to brown; mandibular bases without yellow maculae; labrum entirely black or with small medio-

basal pale spot (in about 50 per cent of specimens); eyes yellow-brown, green or bluish green; flagellum yellow below, dark red to brown above; wing membranes colorless to slightly milky, veins dark red to brown; tegulae usually testaceous; apical tergal areas hyaline, colorless or slightly yellow, basal to hyaline area usually rufescent on at least terga 2 and 3; distitarsi and often basitarsi rufescent; tibial spurs white to pale yellow.

Clypeus as in female; first flagellar segment with minimum length equal to less than two-thirds maximum length and equal to one-tenth or less maximum length of second segment, penultimate segment more than three times as long as broad, flagellum in repose surpassing pterostigma, segments 4-10 without longitudinal lateral depressions; maxillary palpal ratio about 8:5:4:1, last segment occasionally absent. Sculpturing as in female except as follows: mesoscutum with posteromedian area punctures often somewhat more crowded; tergum 1 medially with basal four-fifths punctate, punctures separated mostly by one puncture width; terga 2 and 3 interband zone punctures more abundant; terga 2-4 with apical areas impuctate or virtually so, dulled, with shagreening often more reticular and less transverse, especially in interband zones; sterna moderately shiny, surfaces usually with coarse reticular shagreening. Terminalia as in *M. agilis*.

Hair: White to pale ochraceous; vertex of head and dorsum of thorax usually more ochraceous than elsewhere; metasomal hairs and pubescence entirely pale, as in *M. menuachus* except as follows: tergum 1 with apical area with long, subappressed, relatively simple, pale hairs usually present but not forming dense band hiding margin; tergum 2 with distal pale band narrow, usually half to three-fourths as wide as apical area medially, as long as or longer than apical area laterally, occasionally narrowly interrupted medially; terga 2-4 with apical areas progressively shorter, with abundant long subappressed to suberect, relatively simple, pale hairs. Legs white to pale ochraceous except yellow to reddish yellow on inner surfaces of tarsi and hind tibiae.

Remarks. Dr. Delma Harding of the Zoology and Entomology Department, Iowa State College, Ames, Iowa, has provided the author with an excellent photograph (Fig. 1) of a female bee visiting *Helianthus petiolaris* in Kansas. This bee is most likely the female of *M. coreopsis*.

Bionomics. Out of 1,986 specimens of *M. coreopsis* available for study, 1,061 bear flower labels. These data are summarized in

Table VII and indicate that *coreopsis* is oligolectic on plants of the family Compositae. The bee visits a great variety of composite genera and species for pollen as well as nectar, and shows some preference for the genus *Helianthus* and related genera.

TABLE VII. Summary of Floral Records for *Melissodes coreopsis.*

Plant Data			Records of *M. coreopsis*			
FAMILY	Number of genera	Number of species	Number of collections	Number of females	Number of males	Total number of bees
Compositae:						
Helianthus spp.	1	6	86	211	124	335
Gaillardia spp.	1	1	17	54	14	68
Rudbeckia spp.	1	3	16	44	65	109
Echinacea spp.	1	3	18	36	13	49
Grindelia spp.	1	1	15	22	4	26
Solidago spp.	1	3	15	15	78	93
Aster spp.	1	2	14	38	3	41
Coreopsis spp.	1	2	8	25	3	28
Other genera	19	23	56	77	82	159
Leguminosae	8	12	41	32	43	75
Labiatae	3	5	13	12	30	42
Other families (12)	13	15	31	13	23	36
Totals	51	76	330	579	482	1,061

Type Material. The lectotype female, here designated, of *coreopsis*, collected by Charles A. Robertson at Carlinville, Illinois, June 14, 1902 on *Coreopsis palmata*, is in the collection of the Illinois Natural History Survey at Urbana. The holotype female of *confusiformis* from Fedor, Lee County, Texas, May 6, 1902, is in the collection of the Natural History Museum of the University of Colorado at Boulder. The holotype male of *helianthophila*, collected by T. D. A. Cockerell at Boulder, Colorado, June 16, on *Helianthus*

lenticularis, is in the collection of P. H. Timberlake at the Citrus Experiment Station, Riverside, California.

Distribution. *M. coreopsis* is distributed from Alberta, North Dakota and Minnesota south to Oaxaca in Mexico, east to Indiana and west to Utah and Arizona (Fig. 16). It has been collected from April 11 to November 6. It seems likely that in Texas where *coreopsis* is abundant from April until November there are three generations of bees per year. In Kansas where this bee is active from June until mid-October, there are probably two generations and in North Dakota where the season of activity is limited to July, August and September, there is likely to be only one generation. In addition to the type material, a total of 1,121 females and 865 males have been examined from the localities listed below. Of these 1,986 specimens, 1,140 are from the state of Kansas. Therefore, locality records from that state are given below only as counties in order to conserve space. Localities reported in the literature are included in the list.

ARIZONA: Douglas; Flagstaff (Walnut Canyon); Oak Creek Canyon. ARKANSAS: Desha Co.; Hot Springs; Washington Co. COLORADO: Antonito; Beneva Park; Berkeley; Boulder; Boulder Canyon; Brighton; Buckeye (S. at Horsecreek); Cameron Pass; Canon City; Chimney Gulch; Clear Creek; Colorado Springs; Cory; Cotopaxi; Crook, Logan Co.; Crowley Co.; Denver; Dixon Canyon; Eads; Elbert; Eldora; Estes Park; Fort Collins; Glen Haven; Jim Creek (near Boulder); La Junta; Lamar; Larimer Co.; Limon; Masonville; Mesa Verde; Ovid (3 miles E.); Palmer Lake; Pingree Park, Larimer Co.; Platte Canyon; Portland; Prospect, Weld Co.; Puils Creek, Crowley Co.; Rock Creek, Teller Co.; Rocky Ford; Seibert (13 miles E.); Sterling; Stratton; Ten-sheep Ranch; Timpas; Towner, Kiowa Co.; Trimnath; Valmont (Owens Lake); Virginia Dale; White Rocks (near Boulder). ILLINOIS: Carlinville; Macoupin Co. IOWA: Ames; Buffalo Center (5 miles N. W.); Dickinson Co.; Grundy Co.; Lyon Co.; Onawa; Sioux City. KANSAS: Counties: Anderson; Barton; Bourbon; Butler; Chase; Chautauqua; Cherokee; Cheyenne; Clark; Cloud; Coffey; Cowley; Dickinson; Douglas; Edwards; Ellis; Finney; Ford; Franklin; Gove; Greeley; Greenwood; Hamilton; Harper; Harvey; Hodgeman; Johnson; Kearny; Kiowa; Labette; Lane; Leavenworth; Logan; McPherson; Marion; Marshall; Meade; Mitchell; Montgomery; Morton; Neosho; Norton; Ottawa; Pawnee; Pottawatomie; Pratt; Reno; Republic; Rice; Riley; Rooks; Rush; Russell; Saline; Scott; Sedgwick; Shaw-

nee; Sheridan; Sherman; Smith; Stafford; Stanton; Stevens; Sumner; Thomas; Trego; Wallace; Wichita; Woodson. MINNESOTA: Moorhead; Rock Co.; Roseau Co.; St. Paul; Yellow Medicine Co. MISSOURI: Branson; Chillicothe (6 miles N.); Columbia; Holden; Ozark Lakes; Warsaw. NEBRASKA: Agate, Sioux Co.; Alliance; Box Butte Co.; Brown Co.; Cambridge; Carns; Cedar Bluffs; Crawford; Dunning; Fairmont; Glen, Sioux Co.; Gordon; Haigler; Halsey; Hamlet, Hays Co.; Hardy; Harrison; Hyannis (9 miles S.); Imperial; Kimball; Lincoln; Lodgepole; McCool Jc.; Malcolm; Mitchell; Monroe Canyon, Sioux Co.; North Platte (8 miles W.); Omaha; Pine Ridge, Dawes Co.; Sioux Co.; Wabash; War Bonnet Canyon, Sioux Co.; Weeping Water; West Point. NEW MEXICO: Capitan; Carlsbad Caverns; Corrizozo; Grady; Las Vegas; Maxwell; Rowe; San Jose; Santa Fe (35 miles E.); Sapello. NORTH DAKOTA: Amidon; Beach; Belfield; Bismarck; Dickinson; Fargo; Hatton; Jamestown; Oakes; Ravinia; Williston; Valley City. OKLAHOMA: Ardmore; Caddo; Lawton; Nowata (5 miles N.); Okmulgee; Quapaw; Wagoner (5 miles N.); Waurika; Vinita. SOUTH DAKOTA: Ardmore; Buffalo; Cedar Pass (Badlands); Custer; Custer Co.; Deadwood (10 miles S.); Deerfield; Edgemont; Hot Springs; Interior; Okaton; Slim Buttes; Stanley Co. TEXAS: Adrian; Alford; Alpine (20 miles S.); Atascosa Co.; Austin; Bay City; Bexar Co.; Big Bend National Park; Brazos Co.; Brewster Co.; Chisos Mts. (Big Bend. N. Park); College Station; Corpus Christi; Cotulla; Dalhart (Rita Blanca Lake); Dallas; Del Rio; Denton; Devil's River; Dilley; Eastland Co.; El Paso (15 miles N.); Fedor, Lee Co.; Fort Davis; Fredricksburg; Giddings; Goliad (16 miles E.); Greenville; Guthrie; Harper; Hetty; Hillsboro; Jack Co.; Johnson City (6 miles W.); Kerrville; Ladonia; Lee Co.; Lobo, Culberson Co.; Magnolia; Marfa; Matagorda; Palo Duro Canyon, Randall Co.; Paris; Plano; Poteet; Quemado, Maverick Co.; Roanoke; Rock Island; Romero; Stonewall; Terrell; Victoria; Waco; Wichita Falls; Willis; Wolfe City. UTAH: Lakepoint. WYOMING: Albany Co.; Diamond Ranch, Platte Co.; Grand Teton National Park; Laramie (37 miles E.); Laramie Co.; Summit; Tie Siding. *Canada.* ALBERTA: Lethbridge. *Mexico.* OAXACA: Nochixtlan (7 miles S. E.).

Flower Records. Amphiachyris sp., *A. dracunculoides, Amorpha canescens, A. fruticosa, Aster* sp., *A. ericoides villosis, A. multiflora, A. novaeangliae, A. paniculatus, A. praecatus, Bidens* sp., *B. involucrata, Boltonia asteroides, Chrysopsis* sp., *C. angustifolia, Chrysothamnus graveolus, Cirsium* sp., *Clematis* sp., *Cleome serrulata,*

Cooperia pedunculata, Convolvulus sp., *Coreopsis* sp., *C. grandiflorum, C. palmata, C. tinctoria, Cosmos* sp., *Echinacea* sp., *E. angustifolia, E. pallida, E. purpurea, Erucastrum pollichii, Eryngium* sp., *E. leavenworthii, Eupatorium altissimum, Euphorbia* sp., *Eustoma russellianum, Gaillardia* sp., *G. pulchella, Geranium* sp., *Gossypium herbaceum, Grindelia* sp., *G. squarrosa, Gutierrezia sarothrae, Haplopappus* sp., *Helenium* sp., *H. autumnale, H. laciniatum, H. latifolia, H. nudiflorum, H. tenuifolium, Heterotheca subaxillaris, Helianthus* sp., *H. annuus, H. grosse-serratus, H. maximillianus, H. petiolaris, H. salicifolius, H. tuberosus, Heliopsis helianthoides, Marrubium vulgare, Medicago sativa, Melilotus alba, M. officinalis, Monarda* sp., *M. citriodora, M. pectinata, M. punctata, Nepeta cataria, Opuntia* sp., *O. lindheimeri, O. macrorhiza, Parosela* sp., *Petalostemum* sp., *P. candidum, P. oligophyllum, P. purpureum, Prionopsis* sp., *P. ciliata, Psoralea floribunda, Ratibida* sp., *R. columnaris, R. pinnata, Rudbeckia* sp., *R. amplexicaulis, R. bicolor, R. hirta, R. laciniata, R. triloba, Salsola pestifer, Silphium* sp., *S. perfoliatum, S. speciosum, Solidago* sp., *S. canadensis, S. rigida, S. serotina, Tetragonotheca ludoviciana, Tetraneuris linearifolia, Trifolium repens, Verbena* sp., *V. officinalis, V. stricta, Verbesina encelioides, Vernonia* sp.

Melissodes (Eumelissodes) nivea Robertson

Melissodes nivea Robertson, 1895, Trans. Amer. Ent. Soc., vol. 22, p. 127; 1897, Trans. Acad. Sci. St. Louis, vol. 7, p. 354; 1905, Trans. Amer. Ent. Soc., vol. 31, p. 368; Cockerell, 1907, Ann. Mag. Nat. Hist., ser. 7, vol. 20, p. 128; Robertson, 1928, Flowers and Insects, p. 8; Pearson, 1933, Ecol. Monogr., vol. 3, p. 381; Graenicher, 1935, Ann. Ent. Soc. Amer., vol. 28, p. 304; Brimley, 1938, Insects of North Carolina, p. 462.

Melissodes nivea is closely related to *M. coreopsis*. The females of *nivea* can be distinguished from those of *coreopsis* primarily by the small but distinct punctures in the apical areas of terga 2 and 3 and by the short, white hairs in the same areas. The male is very similar to the male of *M. agilis* in the color of the labrum, mandibles and wing veins, but is like *M. coreopsis* in the extremely short first flagellar segments and in the shiny galeae. The pale pubescence and hairs of both sexes of *nivea* tend to be white, rather than dull ochraceous as in *coreopsis* or rufescent as in *agilis*.

Female. Measurements and ratios: N, 20; length, 9-12 mm.; width, 4.0-4.5 mm.; wing length, $M = 2.84 \pm 0.095$ mm.; hooks in hamulus, $M = 11.30 \pm 0.128$; flagellar segment 1/segment 2, $M = 1.70 \pm 0.019$.

Structure and color: Integumental color as in *coreopsis* except

as follows: wing veins dark red to reddish brown; tergum 1 with apical third occasionally rufescent, apical margin narrowly hyaline.

Structure and sculpturing as in *coreopsis* except as follows: clypeal punctures round, separated by less than half a puncture width, surface shiny with sparse striations, apicomedian longitudinal carina usually present; supraclypeal area usually dulled by reticular shagreening, with scattered coarse punctures; maxillary palpal ratio about 2.5:2.5:2.0:1.0, last segment sometimes slightly shorter. Mesoscutal punctures round, posteromedially deep, larger, separated mostly by one to two puncture widths, anteriorly and laterally slightly smaller, shallow, separated mostly by half a puncture width or less; scutellar punctures similar to posteromedial mesoscutal punctures but more crowded; surfaces of mesoscutum and scutellum shiny, often slightly dulled by fine reticular shagreening; mesepisternal punctures as large as posteromedian mesoscutal punctures; separated by half a puncture width or less, surface shiny, unshagreened or extremely delicately and irregularly so. Metasomal tergum 1 with basal area punctures larger and more crowded, apical impunctate area moderately shiny to shiny, with delicate reticulotransverse shagreening; tergum 2 with interband zone punctures small, deep, relatively regularly spaced, separated by half to one puncture width, apical area with small distinct punctures two to three times as wide as bases of appressed hairs arising from them, surface (especially of apical area) shiny to moderately shiny; tergum 3 similar to 2 but with interband zone and apical area punctures more crowded. Pygidial plate V-shaped with sides diverging posteriorly and apex well rounded, longer than basal breadth.

Hair: Head white with abundant long brown hairs on vertex. Thorax white except mesoscutum with dark brown posteromedian patch often extending forward to a transverse line at anterior margins of tegulae and almost reaching tegulae laterally (darkest in eastern specimens), scutellar hairs dark brown except white fringe, tegulae dark brown, and pale hairs of mesoscutum often pale cinereous. Metasoma as in *coreopsis* except as follows: tergum 2 with distal pale band white, as long as or longer than apical area medially, interband zone hairs mostly dark brown in specimens from Atlantic states and mostly white in specimens from prairie states, apical area with short, relatively simple, appressed to subappressed, white hairs (occasionally a few brown medially in darkest forms); tergum 3 similar to 2 but apical area shorter and often with median hairs brown; tergum 4 with apical white band never interrupted

medially nor fringed apically with brown; terga 5 and 6 with conspicuous lateral white tufts. Legs as in *coreopsis* but inner surfaces hind basitarsi more often reddish brown than darker.

Male. Measurements and ratios: N, 20; length, 9-12 mm.; width, 3-4 mm.; wing length, M = 2.85 ± 0.135 mm.; hooks in hamulus, M = 10.60 ± 0.323; flagellar segment 2/segment 1, M = 10.54 ± 0.183.

Structure and color: Integumental color as in *M. agilis* except as follows: labral pale spot occasionally reduced but never absent, basal mandibular yellow maculae often reduced in size and rarely absent; tergal apices hyaline and colorless.

Structure as in *coreopsis* except as follows: first flagellar segment with minimum length equal to one-tenth or less of maximum length of second segment, penultimate segment slightly longer than three times minimum width, segments 5-10 slightly crenulate when viewed from below, flagallum in repose just reaching pterostigma; maxillary palpal segments in ratio of about 3.5:4.5:3.0:1.0, last segment often slightly longer. Sculpturing as in female except as follows: mesoscutal punctures smaller, often more crowded posteromedially; tergum 1 medially with basal four-fifths punctate; terga 2 and 3 with apical areas not distinctly punctate, shiny. Terminalia as in *agilis,* but sternum 8 with apicoventral tubercle pointed, not bidentate, and slightly surpassing apical margin in apicomedian emargination.

Hair: White except inner surfaces tarsi yellow and occasionally dorsum of thorax slightly cinereous. Metasomal tergum 2 with distal pale band as wide as apical area medially or wider; terga 2 and 3 with apical areas with abundant, suberect to subappressed, relatively simple, white hairs; tergum 1 with pubescent not forming thick apical band hiding margin of tergum.

Bionomics. Of 58 specimens representing 29 collections which have floral data attached, 54 specimens (28 collections) were taken on some species of Compositae. The single collection not from a composite consists of four females taken on *Gerardia* sp. (Scrophulariaceae). *M. nivea* can, accordingly, be considered as an oligolege of composites and has some preference for species of the genera *Solidago, Aster,* and *Liatris* in that order.

Type Material. Lectotype female, here designated, of *nivea,* collected by Charles A. Robertson (Coll. No. 3205) at Carlinville, Illinois, September 8, 1886, on *Solidago lanceolata* is in the collection of the Illinois Natural History Survey at Urbana. The lecto-

allotype male of *nivea,* here designated, collected by Robertson (Coll. No. 17648) at Carlinville, Illinois, August 21, 1895, on *Lepachys pinnata* is also in the Illinois Natural History Survey collection.

Distribution. M. nivea occurs from Long Island, New York, south to North Carolina and Alabama, and west to Minnesota, Kansas, Arkansas and Mississippi (Fig. 17). It has been collected from July 16 to October 14, but chiefly in September. In addition to the type material, a total of 136 females and 91 males have been examined from the localities listed below. This list includes localities reported in the literature.

ALABAMA: Mobile. ARKANSAS: Fort Smith (25 miles N.), Ouachita Mts.; Knob Hill Reservation, Ouachita Mts. DISTRICT OF COLUMBIA: Washington. ILLINOIS: Carbondale; Carlinville; Macoupin

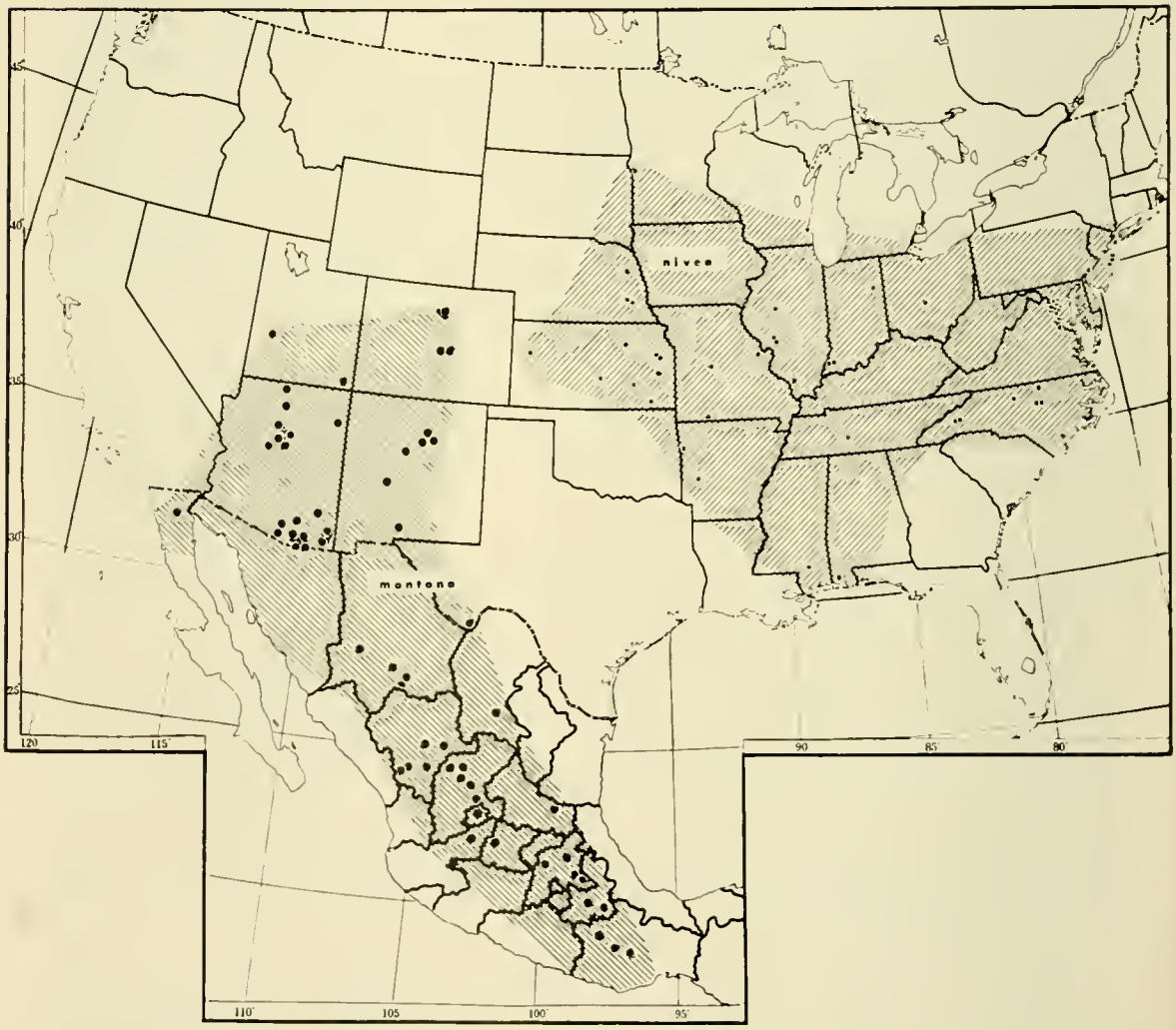


FIG. 17. Map showing the known distributions of *M. (Eumelissodes) nivea* Robertson and *M. (E.) montana* Cresson.

Co.; Manito. INDIANA: Bluffton; Gibson Co.; Rush Branch. KANSAS: Baldwin; Cherryvale (2 miles S.); Douglas Co.; Garnett; Hutchinson; Logan Co.; Reece; Riley Co. MARYLAND: Bethesda; Cabin John; Glen Echo; Indian Head. MINNESOTA: Ortonville. MISSISSIPPI: Camp Shelby (near Hattiesburg). MISSOURI: Branson; Gilmore; Ozark Lake. NEBRASKA: Lincoln; Malcolm; West Point. NEW JERSEY: Asbury Park; Jamesburg; Lakehurst; Lakewood. NEW YORK: Astoria, Long Island. NORTH CAROLINA: Black Mts. (valley of); Burgaw; Crabtree Meadows Park; Greensboro; Oxford; Raleigh; Swannanoa. OHIO: Columbus. PENNSYLVANIA: Darby. TENNESSEE: Maury Co. VIRGINIA: Arlington; Barcroft; Camp Peary; Falls Church; Fort Humphreys; Four-mile Run (near mouth of); Glen Carlyn; Mathias Point; Vienna; Virginia Beach. WISCONSIN: Milwaukee.

Flower Records. Aster sp., *A. ericoides, A. sagittifolius, Bidens laevis, Boltonia asteroides, Chrysopsis mariana, Gerardia* sp., *Helenium* sp., *Helianthus* sp., *H. annuus, H. atrorubens, Lacinaria* sp., *Lepachys pinnata, Liatris graminifolia, Prionopsis ciliata, Solidago* sp., *S. canadensis, S. lanceolata, S. rigida, S. serotina, Vernonia* sp., *V. glauca.*

Melissodes (Eumelissodes) pilleata, n. sp.

This is a medium-sized, black and white bee related both to *M. coreopsis* and to *M. rustica.* The female resembles that of *coreopsis* in sculpturing and in vestiture coloration but can be distinguished by the black fringe of hairs at the apex of tergum 4, the lack of pale lateral tufts on terga 5 and 6, and the broad pygidial plate. The female is readily confused with that of several closely related species whose descriptions follow below. The male is like *rustica* in having the apical tergal areas piceous, but is like *agilis* in having pale spots at the bases of the mandibles and on the labrum, and is like *coreopsis* in the short first flagellar segment and the shiny galeae. Both sexes have the wing membranes slightly infumate.

Female. Measurements and ratios: N, 20; length, 10-14 mm.; width, 3.5-4.5 mm.; wing length, M = 3.27 ± 0.089 mm.; hooks in hamulus, M = 12.60 ± 0.143; flagellar segment 1/segment 2, M = 1.90 ± 0.002.

Structure and color: Integument black except as follows: apical half of mandible, lower surfaces flagellar segments 3-10, and distitarsi rufescent; eyes grayish blue to dark gray; wing membranes somewhat infumate with slight violaceous reflections, veins dark

brown to black; tegulae piceous; tibial spurs yellow to red; tergum 1 with extremely narrow apical margin hyaline or testaceous.

Structure and sculpturing as in *coreopsis* except as follows: clypeus slightly protuberant, oculoclypeal distance equals 0.50 to 0.75 times minimum diameter first flagellar segment, with regular round punctures separated mostly by half a puncture width, smaller and crowded anteriorly, without distinct longitudinal carina, surface moderately shiny, with sparse but distinct striations, supraclypeal area usually with several large deep punctures, surface shiny or slightly dulled by sparse reticular shagreening; galeae unshagreened above except at tips; maxillary palpal ratio about 2.25:2.50: 2.25:1.00, a small fifth segment often present; metasomal tergum 1 with basal three-fifths with relatively large shallow punctures separated mostly by half to one puncture width; tergum 2 with basal area punctures separated mostly by half a puncture width; terga 2 and 3 with apical areas with minute scattered punctures no broader than twice diameter of hairs arising from them; metasomal terga shagreened as in *coreopsis*, but usually shinier; pygidial plate broadly V-shaped, rounded apex, about as broad at base as median length.

Hair: As in *M. nivea* except as follows: more abundant black hairs on vertex of head; mesoscutal dark patch extends forward beyond a transverse line at anterior margins of tegulae and to within one or two hairs of tegulae laterally; scutellum dark brown or black except for peripheral one or two hairs; tergum 2 with distal pale band usually narrower than apical area and often interrupted medially; terga 2 and 3 with apical areas with sparse, simple, appressed, dark brown to black hairs; terga 5 and 6 without lateral pale tufts; tergum 4 with apical fringe of dark brown hairs at least in median third; legs with fore and middle tarsi brown, outer surfaces of fore and middle tibiae brown distally, inner surfaces hind basitarsi dark brown to black, and scopal hairs pale ochraceous.

Male. Measurements and ratios: N, 15; length, 10-12 mm.; width, 3-4 mm.; wing length, $M = 3.12 \pm 0.154$ mm.; hooks in hamulus, $M = 11.20 \pm 0.175$; flagellar segment 2/segment 1, $M = 10.05 \pm 0.699$.

Structure and color: Integument black except as follows: Clypeus pale yellow to cream-colored with testaceous apical margin; labrum white with dark brown margin; mandibles with pale basal maculae similar in color to clypeus; eyes grayish blue to gray; wing membranes slightly infumate, veins dark brown; tegulae piceous;

flagellar segments 2 to 11 rufescent below; distitarsi rufescent; extremely narrow apical margin of tergum 1 hyaline or testaceous; terga 2-5 with apical areas piceous.

Structure as in *coreopsis* except as follows: first flagellar segment with minimum length equal to one-eighth or slightly less of maximum length second segment, third segment distinctly longer than three times minimum diameter, not crenulate, in repose surpassing pterostigma and even marginal cell; maxillary palpal ratio about 3.00:3.33:2.66:1.00, minute fifth segment often present. Sculpturing as in female except as follows: posteromedian mesoscutal punctures more crowded; tergum 1 with basal four-fifths punctate, punctures become progressively smaller and sparser as they approach narrow apical impunctate area; terga 2 and 3 with interband zone punctures smaller and sparser, apical areas virtually impunctate, surfaces shiny to moderately so. Pygidial plate slightly longer than broad. Terminalia as in *agilis* but sternum 8 with ventral tubercle pointed, not bidentate, and weak, and gonostyli with few hairs basally.

Hair: White except as follows: vertex of head dark brown; dark brown mesoscutal patch extends forward to a transverse line at anterior margins of tegulae and laterally to within 5 or 6 hair-rows of tegulae; scutellum dark brown except peripherally. Metasomal vestiture as in female except as follows: tergum 1 with apical third with progressively shorter, relatively simple, suberect to subappressed, dark brown hairs; terga 2 and 3 with distal pale bands somewhat narrower, rarely interrupted medially; tergum 4 similar to 3 but apical area reduced to narrow fringe of brown; tergum 5 with distal pale band reaching apex medially; terga 6 and 7 with dark brown hairs. Legs white except inner surfaces tarsi and hind tibiae yellow.

Type Material. The holotype male collected by T. B. Mitchell at Southern Pines, North Carolina, September 23, 1950, on *Kuhnistera* sp. is in the collection of T. B. Mitchell, North Carolina State College, Raleigh. The allotype female from Southern Pines, North Carolina, September 16, 1918, on *Gerardia flava* is in the collection of the American Museum of Natural History, New York City. Eighteen female and twelve male paratypes from North Carolina and collected by T. B. Mitchell are as follows: Aberdeen: 1 female and 1 male, September 10, 1923; 1 female and 1 male without floral data and 2 females on *Gerardia* sp., September 26, 1923; 1 female, October 15, 1957. Raleigh: 3 males in August (no further

collection data). Southern Pines: 2 females on *Gerardia* sp. and 1 female on *Liatris* sp., September 26, 1923; 1 male on *Kuhnistera pinnata*, September 15, 1949; 2 males on *Kuhnistera* sp., September 10, 1950; 1 female on *Chrysopsis* sp., September 23, 1950; 3 females without floral data, 1 female on *Aster* sp., and 1 female on *Kuhnistera* sp., September 30, 1951; 1 male, September 13, 1952; 1 female without floral data and 1 female on *Kuhnistera* sp., September 19, 1953; 2 females on *Chrysopsis* sp., October 15, 1957. Two female and three male paratypes from Southern Pines, North Carolina, were collected as follows: 2 males on *Aster* sp., August 20, 1918; 1 male, August 29, 1918; 2 females, September 13, 1918. Paratypes are in the collections of T. B. Mitchell, the American Museum of Natural History, the Snow Entomological Museum of the University of Kansas, Lawrence, and in the author's collection (Fig. 16).

Melissodes (Eumelissodes) confusa Cresson

Melissodes confusa Cresson, 1878, Proc. Acad. Sci. Philadelphia, vol. 30, p. 205; Cockerell, 1897, New Mexico Coll. Agr. and Mech. Arts, Bull. No. 24, pp. 20, 24; Birkman, 1899, Ent. News, vol. 12, p. 43; Bridwell, 1899, Trans. Kansas Acad. Sci., vol. 16, p. 211; Viereck, 1902, Trans. Amer. Ent. Soc., vol. 29, p. 46; Cockerell, 1906, Trans. Amer. Ent. Soc., vol. 32, pp. 82, 92; 1906, Trans. Amer. Ent. Soc., vol. 32, p. 309; 1906, Bull. Amer. Mus. Nat. Hist., vol. 22, pp. 443, 454; Snow, 1906, Trans. Kansas Acad. Sci., vol. 20, p. 137; Cockerell, 1910, Psyche, vol. 17, p. 246; 1911, Canadian Ent., p. 43, p. 33; Cresson, 1916, Mem. Amer. Ent. Soc., vol. 1, p. 116; Rau, 1922, Trans. Acad. Sci. St. Louis, vol. 24, p. 34; Cockerell, 1933, Ann. Ent. Soc. Amer. vol. 26, p. 44; Bohart, Knowlton and Bailey, 1950, Utah St. Agric. Coll. Mimeo. Ser. No. 371, p. 5.

Melissodes ruidosensis Cockerell, 1896, Entomologist, vol. 29, p. 305; 1898, Bull. Sci. Lab. Denison Univ., vol. 11, p. 66; 1898, Bull. Univ. New Mexico, vol. 1, p. 66; 1901, Ent. News, vol. 12, p. 43; 1901, Ann. Mag. Nat. Hist., ser. 7, vol. 7, p. 130; 1902, Amer. Nat., vol. 36, p. 810; 1903, Ann. Mag. Nat. Hist., ser. 7, vol. 12, p. 450.

Melissodes tenuitarsis Cockerell, 1905, Psyche, vol. 12, p. 99 (new synonymy); 1906, Trans. Amer. Ent. Soc., vol. 32, p. 76; Snow, 1906, Trans. Kansas Acad. Sci., vol. 20, p. 137.

Melissodes civica Cockerell, 1910, Ann. Mag. Nat. Hist., ser. 8, vol. 5, p. 258 (new synonymy).

Melissodes atraticornis Cockerell, 1934, Amer. Mus. Nov. No. 697, p. 9 (new synonymy).

This species is highly variable in both sexes, a fact which makes it difficult to identify and has contributed to the synonymy. It is perhaps most closely related to *M. coreopsis*, but also shows some structural affinity to *M. grindeliae* and *M. rustica*. The female of *confusa* is similar to that of *coreopsis* but is darker in color as follows: terga 4 and 5 usually without pale lateral hair tufts, sternal hairs usually dark brown, often with lower and anterior surfaces of mesepisterna with brown hairs. In both sexes the antennae are often wholly black, although this is not so frequent in males as in

females. The female can be distinguished from that of *grindeliae* by the punctation of the basal area of tergum 2 as described below. The male has the short first flagellar segment of *coreopsis*, although often slightly longer, but has shorter antennae as a whole. The male clypeus varies in color from entirely yellow except the testaceous apical margin to almost entirely black. The basal area punctures of tergum 2 are sparse as in the female.

Female. Measurements and ratios: N, 20; length, 11-13 mm.; width, 3.5-5.0 mm.; wing length, M = 3.54 ± 0.211 mm.; hooks in hamulus, M = 12.70 ± 0.219; flagellar segment 1/segment 2, M = 1.86 ± 0.013.

Structure and color: Integument as in *coreopsis* except as follows: distitarsi black to dark red; eyes gray to dark gray; flagellar segments 3 to 10 dark reddish brown to black below, second segment entirely dark; wing membranes somewhat infumate, brownish yellow; veins black to dark brown; tibial spurs yellowish to red.

Sculpturing and structure of head and thorax as in *coreopsis* except as follows: clypeus slightly protruding forward beyond eyes, oculoclypeal distance half to three-fourths minimum width of first flagellar segment, punctures slightly more coarse; supraclypeal area usually with surface shiny, unshagreened; maxillary palpal ratio about 3.0:2.7:2.0:1.0. Metasomal tergum with basal three-fifths or slightly less with shallow, medium-sized punctures separated mostly by half to two puncture widths, apical zone extended to form anterolateral impunctate lobes; tergum 2 with basal area punctures round, small, deep, separated by one to two puncture widths or slightly more, surface unshagreened or with delicate reticular shagreening, apical area with small punctures about twice diameter of hairs arising from them, surface dulled by reticulotransverse shagreening, but moderately shiny to shiny. Pygidial plate broadly V-shaped with rounded apex, length subequal to basal width to slightly longer.

Hair: Head as in *coreopsis*. Thorax as in *coreopsis* except as follows: pale hairs ochraceous above, white to pale ochre laterally; mesepisterna with anterior, ventral and lower lateral surfaces usually dark brown; posteromedian dark mesoscutal patch twice as large as scutellar dark patch or larger, usually almost reaching tegulae laterally and extending forwards beyond a transverse line at anterior margins of tegulae; tegulae with dark hairs. Metasomal tergum 1 with basal area white to ochraceous, often quite yellow, apical area with minute, closely appressed, brown hairs at least

basally; tergum 2 with distal pale pubescent band pale ochraceous to yellowish, usually reaching apex of tergum laterally, shorter medially but rarely interrupted, interband zone with abundant, erect to suberect, dark brown hairs, apical area with abundant, suberect to subappressed, dark brown, relatively simple hairs in basal two-thirds; tergum 3 as tergum 2 but basal area dark brown, distal pale band longer and reaching apex in lateral thirds or more; tergum 4 as in *coreopsis;* terga 5 and 6 without lateral pale tufts; sterna reddish brown to dark brown. Legs ochraceous except as follows: distitarsi, fore and middle basitarsi brown or largely so; middle basitarsi with inner surface dark reddish; hind basitarsi with inner surfaces reddish brown to black; scopal hairs often yellowish; basitibial plates, outer apical surfaces fore and middle tibiae brown; hind tibiae with inner surfaces yellow to dark red.

Male. Measurements and ratios: N, 20; length, 9-12 mm.; width, 2.5-4.0 mm.; wing length, M = 3.51 ± 0.156 mm.; hooks in hamulus, M = 12.10 ± 0.169; flagellar segment 2/segment 1, M = 6.08 ± 0.163.

Structure and color: Integumental color as in *coreopsis* except as follows: clypeus varies from yellow with testaceous apical margin and dark maculae at tentorial pits to entirely black, most often yellow with dark brown apical margin and infuscated along posterior margin between and slightly beyond tentorial pits; labrum and mandibles black; eyes dark gray to yellowish green; flagellum varies from red below and dark brown above with first segment entirely dark to entire flagellum dark brown or black, most often with first segment, base of second segment, tip of last segment and upper surfaces dark brown and red below; wing membranes slightly infumate, yellowish; veins dark brown to black; metasomal terga with apical areas hyaline, yellowish brown to yellow, not rufescent basally; distitarsi rufescent; tibial spurs yellow.

Clypeus much as in female; first flagellar segment with minimum length equal to almost half maximum length and equal to about one-eighth maximum length second segment, penultimate segment one-third as wide as long or slightly broader, just reaching pterostigma or slightly less in repose, flagellum somewhat crenulate near apex in lateral view (involving penultimate three to five segments); maxillary palpal ratio about 2.7:1.7:2.0:1.0. Sculpturing as in female except as follows: mesoscutal punctures often more crowded; metasomal tergum 1 with basal four-fifths punctate; terga 2 and 3 with interband zone punctures more distinct and often slightly

larger, apical area punctures minute or absent; tergum 2 with basal area punctures minute, separated by two to four puncture widths and mostly by three or four widths; sterna shiny; reticular shagreening coarse, often absent medially. Terminalia as in *M. agilis,* but sternum 8 with abundant apical hairs and with apicomedial tuft of hairs just above ventral tubercle, tubercle acute, not bidentate.

Hair: Head and thorax pale to dark ochraceous, paler laterally, head often with brown on vertex, mesoscutum often with dark brown patch posteromedially, scutellum usually with at least a few brown hairs, tegulae usually with brown. Metasomal tergum 1 pale to dark ochraceous except two or three subapical rows of shorter, relatively simple, dark brown hairs; tergum 2 pale ochraceous to white basally, distal band ochraceous, arched medially but usually not interrupted, basal and distal bands connected laterally, interband zone hairs suberect to erect, yellow to dark brown, apical area hairs subappressed to suberect, dark brown to ochraceous (usually at least apical few rows dark); terga 3 and 4 similar but basal tomentum brown, interband zone hairs more often and mostly dark brown, apical areas progressively shorter; tergum 5 like tergum 4 but distal pale band apical; terga 6 and 7 entirely dark brown to dark medially and ochraceous to light brown laterally. Legs ochraceous except yellowish orange on inner surfaces tarsi and basitibial plates brown.

Bionomics. The floral data for this species are sparse, but they indicate the usual oligolecty of the subgenus *Eumelissodes,* that is, a preference for flowers of the family Compositae as pollen sources. A wide variety of composites are visited, however, and it is difficult to state any preference on the basis of the present data. However, *M. confusa* is unsual in that it has not yet been collected visiting flowers of *Helianthus.* Also, the author has collected males on more than one occasion (especially in Mexico) sleeping in the flowers of *Argemone* (Papaveraceae), but no females have been taken from this flower. Table VIII below summarizes the floral data.

Type Material. Lectotype female and lectoallotype male of *confusa,* both from Colorado, are in the Academy of Sciences of Philadelphia, Pennsylvania. Cockerell apparently did not designate a holotype for his *M. ruidosensis.* However, I have seen several specimens labeled *ruidosensis* in Cockerell's handwriting and Lutz and Cockerell synonymize *ruidosensis* with *confusa* in their catalogue (1920). Two males labeled as cotypes of *ruidosensis* were

TABLE VIII. Summary of Floral Records for *Melissodes confusa.*

Plant Data			Records of *M. confusa*			
FAMILY	Number of genera	Number of species	Number of collections	Number of females	Number of males	Total number of bees
Compositae:						
Cirsium spp.	1	2	15	19	27	46
Helenium spp.	1	3	8	21	70	90
Grindelia sp.	1	1	9	11	1	12
Other Genera	14	19	27	39	17	56
Leguminosae	4	4	8	3	8	11
Labiatae	3	3	5	5	3	8
Geraniaceae	1	1	4	6	2	8
Other Families (7)	7	7	9	5	13	18
Totals	32	40	83	109	141	250

found in the collection of the U. S. National Museum, Washington, D. C. I hereby designate one of these (Cotype No. 3361) as the lectotype male of *ruidosensis.* This male also bears the label "Wooton 111." The holotype male of *tenuitarsis* from Oak Creek Canyon, Arizona, collected by F. H. Snow, is in the Snow Entomological Museum of the University of Kansas, Lawrence. The female holotype of *civica,* collected by Farrar at Mexico City, Mexico, is in the Zoologische Museum der Humboldt Universität, East Berlin, Germany. The holotype male of *atraticornis* from Pingree Park, Colorado, collected by Louise Ireland on August 14, 1933, is in the Academy of Sciences of Philadelphia, Pennsylvania.

Distribution. M. confusa ranges from southern Canada to central Mexico and from California to Wyoming and Minnesota (Fig. 18). It has been taken from June 23 to September 21, but chiefly during July and early August in the United States, and as late as December 11 in central Mexico. A total of 272 females and 570 males have been examined from localities listed below. As this species has in the past been confused with several other species, only those published records which have been verified by the author

FIG. 18. Map showing the known distribution of *M. (Eumelissodes) confusa* Cresson.

are included in the list. This omits certain dubious records in Kansas, Missouri, Texas and Illinois.

ARIZONA: Baboquivari Mts.; Barfoot Camp Grounds, Chiricahua Mts.; Deer Park, Chiricahua Mts.; Flagstaff (and 4 miles N., 7 miles S. and 6 miles W.); Globe; Graham Mts.; Grand Canyon; Hospital Flat, Pinaleno Mts.; Houserock Canyon; Humphrey's Peak; Kaibab Forest; Leukachuka Mts.; McNary; Madera Canyon, Santa Rita Mts.; Mt. Lemmon, Santa Catalina Mts.; Oak Creek Canyon; Onion Saddle, Chiricahua Mts.; Paradise (4 miles W.), Chiricahua Mts.; Ramsey Canyon, Huachuca Mts.; Rustler's Park, Chiricahua Mts.; San Francisco Mt.; Santa Catalina Mts.; Sierritas (Black Dike Prospect); Vail Lake; White Mts.; Williams. CALIFORNIA: Big Bear Lake, San Bernardina Co.; Huntington Lake, Fresno Co.; Little Pine Valley, Mono Co.; Yosemite Valley. COLORADO: Aspen; Boulder; Buena Vista; Chimney Gulch (Golden); Cimarron; Colorado Springs; Costillo; Creede; Estes Park; Florissant; Gilpin (Lump Gulch); Glen Haven; Jim Creek (near Boulder); Leadville; Manitou Park; Meeker; Mesa Verde; Monument Lake; Ouray; Pagosa Springs; Peaceful Valley; Pingree Park; Ridgway; Rosa Mts.; San Luis Valley; San Miguel Mts., Wilson Peak; St. Vimis Creek (above Peaceful Valley); Tolland; Villa Grove; Ward; Westcliff. MINNESOTA: Ada; Alma Township (east of Argyle); Hastings; Kittson Co.; Middle River; Plummer; Red Lake Co.; Roseau Co. NEVADA: Charleston Peak, Clark Co.; Kyle Canyon, Charleston Mts. NEW MEXICO: Albuquerque; Beulah; Dripping Springs, Organ Mts.; Las Vegas; Ruidoso Creek; Santa Fe; Sapello; Sapello Canyon; White Mts. (several locales in, including Rio Ruidoso); Willow Canyon. NORTH DAKOTA: Fargo; Grand Forks; Granville; Jarves Lake, Turtle Mts.; Kensal; Dakota; Minot; Mylo; Nicholson; Stanley; Perth; Wales. UTAH: Escalante (15 and 22 miles N.); Glendale; Heber (12 miles S. E.); Kanab; Ogden; Mt. Timpanogos. WYOMING: Summit; University of Wyoming Summer Camp. *Canada.* ALBERTA: Lethbridge. MANITOBA: Shoal Lake; Teulon; Transcona. SASKATCHEWAN: Earl Grey; Saskatoon; Swift Current. *Mexico.* BAJA CALIFORNIA: ?"BC"? CHIHUAHUA: Minaca (22 miles S.). COAHUILA: Buena Vista (Sierra del Carmen). DISTRITO FEDERAL: Atlacomulco; Toluca (20 miles E.; 22 miles N.). DURANGO: Coyote; El Salto (and 6 miles N. E., and 25 miles S. W.); Palos Colorados. HIDALGO: Pachuca (and 16 miles E.). MICHOACAN: Tancitaro. MORELOS: Cuernavaca (19 miles N.). OAXACA: Monte Alban. VERACRUZ: Jalapa (13 miles N. W.); Perote (9 miles N.).

Flower Records. *Agoseris glauca, Aplopappus* sp., *Argemone* sp., *A. platyceras, Aster* sp., *A. canescens, Bidens triplinervia* var. *macracantha, Ceanothus* sp., *Cirsium* sp., *C. undulatum, Cleome* sp., *Cosmos parviflorus, Erigeron* sp., *E. uniflorus, Eryngium asperum, Gaillardia* sp., *Geranium* sp., *G. atropurpureum, Grindelia* sp., *G. squarrosa, Helenium* sp., *H. bigelovii, H. hoopseii, Heliopsis scabra, Lactuca pulchella, Lotus* sp., *Medicago sativa, Monarda* sp., *M. pectinata, Penstemon* sp., *Petalostemum purpureum, Phacelia* sp., *Polymentha* sp., *Ratibida columnaris, Rudbeckia* sp., *R. hirta, R. lacinita, Senecio bigelovii, S. purchianus, Solidago* sp., *S. trinervata, Teucrium occidentale, Verbena stricta, Verbesina* sp., *V. enceliodes, Vicia* sp., *V. pulchella.*

Melissodes (Eumelissodes) montana Cresson

Melissodes montana Cresson, 1878, Proc. Acad. Nat. Hist. Philadelphia, vol. 30, p. 202; Townsend, 1896, Canadian Ent., vol. 28, p. 139; Cockerell, 1896, Entomologist, vol. 29, p. 308; 1897, Entomologist, vol. 40, pp. 21, 24, 28; 1897, New Mexico Coll. Agric. and Mech. Arts, Bull. No. 24, p. 21; 1898, Bull. Sci. Lab. Denison Univ., vol. 11, p. 66; Bull. Univ. New Mexico, vol. 1, p. 66; Birkman, 1899, Ent. News, vol. 10, p. 245; Viereck, 1903, Proc. Acad. Nat. Sci. Philadelphia, vol. 54, p. 728; Cockerell, 1903, Psyche, vol. 10, p. 77; 1906, Trans. Amer. Ent. Soc., vol. 32, pp. 78, 88, 92; 1906, Trans. Amer. Ent. Soc., vol. 32, p. 309; Snow, 1906, Trans. Kansas Acad. Sci., vol. 20, p. 137; Cresson, 1916, Mem. Amer. Ent. Soc., vol. 1, p. 124.

Melissodes hirsuta Smith, 1879, Desc. new species in the Collection of the British Museum, p. 116 (new synonymy); Cockerell, 1905, Trans. Amer. Ent. Soc., vol. 31, p. 328.

Melissodes atrifera Cockerell, 1910, Ann. Mag. Nat. Hist., ser. 8, vol. 5, p. 256 (new synonymy).

Melissodes atrifera sandiarum Cockerell, 1910, Ann. Mag. Nat. Hist., ser. 8, vol. 5, p. 257 (new synonymy); 1911, Trans. Amer. Ent. Soc., vol. 37, p. 239.

M. montana is closely related to *M. coreopsis* from which it is difficult to distinguish, especially in the female sex. The female of *montana* is slightly darker than that of *coreopsis*, has black wing veins, and has red to reddish brown hairs on the inner surfaces of the hind basitarsi. The flagellum tends to be entirely black or dark brown below, as well as above, unlike the paler flagellum of *coreopsis*. The male differs from that of *coreopsis* by having abundant dark hairs on the abdomen, and usually on the mesoscutum, scutellum, tegulae and vertex of the head. *M. montana* is also related to *M. confusa* from which it can be separated in both sexes by the more coarse and crowded punctures at the base of the second metasomal tergum. In addition the female of *montana* usually has tufts of pale hairs at the sides of tergum 5 and often tergum 6 and apically across the penultimate sternum.

Female. Measurements and ratios: N, 20; length, 11-14 mm.; width, 4.0-4.5 mm.; wing length, M = 3.65 ± 0.133 mm.; hooks in

hamulus, M = 13.90 ± 0.204; flagellar segment 1/segment 2, M = 1.85 ± 0.028.

Structure and color: Integument as in *coreopsis* except as follows: basitarsi and tibiae not rufescent; flagellar segment 3 often brown below and segments 4 to 10 often entirely dark; eyes greenish gray to dark gray; wing membranes slightly infumate to slightly milky, veins black to dark brown; tegulae piceous; tergum 1 with apical margin narrowly hyaline, not rufescent basally.

Clypeus and sculpturing as in *coreopsis* with the following differences: clypeal punctures often coarser, crowded; supraclypeal area often shiny and unshagreened; maxillary palpal ratio about 2.7:2.0:1.7:1.0. Mesoscutal punctures of posteromedian area separated mostly by one to two puncture widths; mesepisternal punctures about equal in size to posteromedial mesoscutal punctures, separated mostly by half a puncture width. Metasomal tergum 1 with basal area punctures separated mostly by one puncture width; tergum 2 with basal area with small round punctures separated mostly by one puncture width, often less, surface usually slightly dulled by reticular shagreening; interband zone punctures small, separated mostly by two puncture widths, apical area impunctate or with minute punctures in basal half; pygidial plate distinctly longer than basal breadth.

Hair: In general as in *coreopsis* with the following differences: mesoscutal dark patch usually larger, usually twice as large as scutellar dark patch or larger, pale hairs anterior to dark patch usually dark ochraceous; tegulae with abundant dark brown hairs; mesepisterna occasionally with a few light brown hairs ventrally; metasomal tergum 1 with apical area and anterolateral impunctate lobes usually with short, relatively simple, closely appressed brown hairs; tergum 2 with interband zone hairs short, subappressed to erect, apical area with short subappressed, dark brown hairs, pale distal band often not notched medially, usually at least notched and interrupted when worn, not reaching apex of tergum laterally; tergum 3 with distal pale band often reaching tergum laterally; tergum 5 almost always and tergum 6 often with small pale lateral tufts; sterna dark reddish brown, often pale laterally, penultimate sternum with apical fringe of ochraceous to white hairs; distitarsi often brown (especially anterior); anterior and middle basitarsi with outer surfaces brown (midbasitarsi occasionally ochraceous); scopal hairs pale to bright ochraceous; inner surfaces hind basitarsi red to reddish brown, usually paler than in either *coreopsis* or *confusa*.

Male. Measurements and ratios: N, 20; length, 10-13 mm.; width, 2.5-4.0 mm.; wing length, M = 3.45 ± 0.138 mm.; hooks in hamulus, M = 12.10 ± 0.240; flagellar segment 2/segment 1, M = 6.67 ± 0.186.

Structure and color: Integument as in *coreopsis* except as follows: eyes usually greenish gray; clypeus yellow with anterior margin brown to testaceous; labrum and mandibles black, rarely with mediobasal pale labral spot; first flagellar segment brown; wing membranes often slightly infumate, veins deep reddish brown to black; apical tergal areas hyaline, yellowish, not rufescent basally.

Clypeus as in female; first flagellar segment as in *coreopsis* but slightly longer, penultimate segment longer than three times width, flagellum surpassing pterostigma in repose; maxillary palpal ratio about 4.0:2.5:3.0:1.0. Sculpturing as in female except as follows: tergum 1 with basal three-fifths or more punctate, punctures progressively smaller distally; terga 2-4 with interband zone punctures slightly coarser and with distal area impunctate; apices of terga moderately shiny; sterna as in *coreopsis.* Terminalia as in *M. agilis.*

Hair: White to pale ochraceous except as follows: vertex of head usually with a few to many brown hairs; mesoscutum usually with brown hairs posteromedially, often abundant; tegulae often with brown hairs; scutellum almost always with a few brown medially; terga 1-4 usually with subappressed to suberect, relatively simple, brown hairs apically; interband zones of terga 3-5 and usually 2 with abundant suberect to erect brown hairs; terga 6 and 7 usually brown or golden brown; sterna brown to red medially, paler laterally; legs with inner surfaces tarsi and hind tibiae yellow to orange.

Remarks. M. montana has in the past been confused with *M. coreopsis, M. confusa* and *M. grindeliae,* especially in the female sex. Females are still difficult to separate from those of *coreopsis,* although excellent characters will differentiate them from *confusa* and *grindeliae.* If the males of *montana* and *coreopsis* were not so distinct, and if the two forms did not overlap over so large a territory without intergrading, one would be tempted to consider one as the subspecies of the other. It is perhaps significant that where *montana* is abundant *coreopsis* is quite rare, with the possible exception of Colorado wherein both species are reasonably abundant.

This species is an oligolege of the Compositae like most other *Eumelissodes.* Of 34 collections (48 females and 22 males) with floral data, 26 collections (35 females and 13 males) are from some

composite. Not enough data are available for more complete analysis than this.

Type Material. Lectotype female of *montana* from Colorado is in the collection of the Academy of Sciences of Philadelphia. A female paratype deposited with the lectotype is actually *M. grindeliae* and two male paratypes with the latter are both *M. gilensis.* The male holotype of *atrifera,* collected in Mexico by Deppe, is in the collection of the Zoologische Museum der Humboldt Universität, East Berlin, Germany. The holotype of *atrifera* has the clypeus wholly infuscated. The holotype male of *atrifera sandiarum,* from the Sandia Mts., New Mexico, collected on *Croton* sp., July 26, 1909, is in the collection of P. H. Timberlake at the Citrus Experiment Station, Riverside, California.

Distribution. This species is known from Colorado and Utah south to Oaxaca and Baja California in Mexico (Fig. 17). It has been collected from June 26 to October 14, but chiefly in August and September. The following list includes all localities from which the author has examined specimens; published records not verified are omitted. A total of 136 females and 134 males have been examined.

ARIZONA: Baboquivari Mts.; Canelo; Carr Canyon, Huachuca Mts.; Chiricahua National Monument; Douglas; Flagstaff; Ganado; Mt. Graham; Grand Canyon; Grand Canyon Junction (4 miles N.); Houserock Canyon; Lochiel (4 miles E.); Madera Canyon, Santa Rita Mts.; Miller Canyon, Huachuca Mts.; Oak Creek Canyon; Onion Saddle, Chiricahua Mts.; Painted Canyon, Cave Creek, Chiricahua Mts.; Palmerlee; Pima Co.; Portal (5 miles W.); Prescott; Ramsey Canyon, Huachuca Mts.; Rustler's Camp, Chiricahua Mts.; Sabino Canyon, Santa Catalina Mts.; San Francisco Mt.; Santa Rita Mts.; Sedona (15 miles N.); Sunnyside Canyon, Huachuca Mts.; Todd's Lodge, Oak Creek Canyon; Walnut Canyon (near Flagstaff). COLORADO: Boulder Canyon; Chimney Gulch; Colorado Springs; Jim Creek (near Boulder); Manitou; Peaceful Valley; Rock Creek, Teller Co. NEW MEXICO: Beulah; Hollywood; Las Vegas; Magdalena Mts.; Organ Mts.; Pecos; Sandia Mts. TEXAS: Big Bend National Park. UTAH: Beaver Ridge Mts.; Big Cottonwood Canyon, Wasatch Mts. (near Bench); Bluff. *México.* AGUASCALIENTES: Aguascalientes (30 miles N.); Rincon de Romos (12 km. N.). BAJA CALIFORNIA: La Laguna, Sierra Laguna. CHIHUAHUA: Minaca (22 miles S.); Ojito (36 km. from Santa Barbara); Salaíces; Santa Barbara. COAHUILA: Cabos. DURANGO: Coyotes; El Salto (6 miles

N. E.); Nombre de Dios; Otinapas; Palos Colorados; San Juan del Río; Villa Ocampo; Yerbanis (Cuencame District). GUANAJUATO: Leon (7 miles N. W.). HIDALGO: Actopán; Huichapán (7 miles S. W.); Ixmiquilpan (19 miles W.); Pachuca. JALISCO: Jalostotitlan (6 miles N. E.). OAXACA: Nochixtlan (7 miles S. E.); Oaxaca; Tamazulapan (4 miles S. E.). PUEBLA: Puebla; Tepanco de Lopez (4 miles N. W.). SAN LUIS POTOSÍ: Cuidad del Maiz (13 miles N. W.). ZACATECAS: Canutillo; Fresnillo (and 9 miles S. E.); Sain Alto; Sombrerete (15 km. E.).

Flower Records. *Aplopappus gracilis, Asclepias* sp., *Aster* sp., *A. commutatus, Croton* sp., *Erigeron* sp., *Eriogonum* sp., *Grindelia* sp., *Gutierrezia* sp., *Helianthus* sp., *H. annuus, Heterotheca subaxillaris, Polymentha* sp., *Senecio longilobus, Verbesina exauriculata.*

Melissodes (Eumelissodes) tristis Cockerell

Melissodes tristis Cockerell, 1894, Ent. News, vol. 5, p. 234; 1896, Entomologist, vol. 29, p. 304; 1897, New Mexico Coll. Agric. and Mech. Arts, Agric. Bull. No. 24, p. 23; 1898, Bull. Sci. Lab. Denison Univ., vol. 11, p. 66; 1898, Bull. Univ. New Mexico, vol. 1, p. 66; 1899, Entomologist, vol. 32, p. 156; 1900, Entomologist, vol. 32, p. 218; 1901, Ent. News, vol. 12, p. 40; 1902, Entomologist, vol. 35, p. 177; 1906, Trans. Amer. Ent. Soc., vol. 32, pp. 75, 92; Viereck, 1906, Trans. Amer. Ent. Soc., vol. 32, pp. 238, 240; Snow, 1906, Trans. Kansas Acad. Sci., vol. 20, p. 137; Cockerell, 1907, Ent. News, vol. 18, p. 397; 1923, Proc. U. S. Nat. Mus., vol. 63, p. 3; 1925, Ann. Mag. Nat. Hist., ser. 9, vol. 16, p. 229; Cresson, 1928, Mem. Amer. Ent. Soc., vol. 5, p. 71; Sperry and Andrews, 1937, Bull. S. California Acad. Sci., vol. 36, p. 108; Bohart, Knowlton and Bailey, 1950, Utah St. Agric. Coll., Mimeo. Ser. No. 371, p. 5.

Melissodes pallidicincta Cockerell, 1896, Entomologist, vol. 29, p. 306; 1897, New Mexico Coll. Agric. and Mech. Arts, Agric. Bull. No. 24, p. 20; 1898, Bull. Sci. Lab. Denison Univ., vol. 11, p. 67; 1898, Bull. Univ. New Mexico, vol. 1, p. 67; 1901, Ent. News, vol. 12, pp. 40, 43; 1901, Ann. Mag. Nat. Hist., ser. 7, vol. 7, p. 130; 1903, Ann. Mag. Nat. Hist., ser. 7, vol. 12, p. 449; 1904, Entomologist, vol. 37, p. 8; 1906, Trans. Amer. Ent. Soc., vol. 32, pp. 88, 92, 109; 1906, Trans. Amer. Ent. Soc., vol. 32, p. 309; 1906, Bull. Amer. Mus. Nat. Hist., vol. 22, p. 443; Snow, 1906, Trans. Kansas Acad. Sci., vol. 20, p. 137; Cockerell, 1907, Ent. News, vol. 18, p. 397; 1907, Univ. Colorado Studies, vol. 4, p. 255; Bray, 1917, Pomona Jour. Ent. Zoo., vol. 9, p. 94; Cockerell, 1925, Ann. Mag. Nat. Hist., ser. 9, vol. 16, p. 229; 1928, Univ. Colorado Studies, vol. 16, p. 114.

Melissodes tristis var. *malvina* Cockerell, 1902, Entomologist, vol. 35, p. 177.

Melissodes semitristis Cockerell, 1905, Psyche, vol. 12, p. 102 (new synonymy); 1906, Trans. Amer. Ent. Soc., vol. 32, p. 75; Snow, 1906, Trans. Kansas Acad. Sci., vol. 20, p. 137.

Melissodes pallidicincta var. *erythrina* Cockerell, 1925, Ann. Mag. Nat. Hist., ser. 9, vol. 16, p. 231; 1928, Univ. Colorado Studies, vol. 16, p. 114.

M. tristis is a distinctive species not closely related to any of the foregoing species, but perhaps most closely to *M. coreopsis.* The males are distinctive in having a completely black clypeus, pale eyes, pale and extremely long flagella, and opaque-white pubes-

cence. The female has a wider clypeus than usual with a marked shiny boss anteromedially, generally white or pale ochraceous pubescence, and a broad, hyaline, colorless, apical margin on the first tergum.

Female. Measurements and ratios: N, 20; length, 10-14 mm.; width, 3.5-5.0 mm.; wing length, M = 3.88 ± 0.182 mm.; hooks in hamulus, M = 13.25 ± 0.190; flagellar segment 1/segment 2, M = 1.86 ± 0.086.

Structure and color: Integument black except as follows: distitarsi and apical half of mandibles rufescent; flagellar segments 3 to 10 and often apex of 2 red below; eyes bluish to greenish gray; wing membranes colorless, often milky, veins reddish brown to black; tegulae piceous; metasomal tergum 1 with apical eighth hyaline, colorless, often slightly rufescent basal to hyaline area; terga 2-4 often with apical areas slightly rufescent; tibial spurs white.

Clypeus flat, broad and short, oculoclypeal distance equals almost three-fourths minimum diameter first flagellar segment and usually more than one-half, with pronounced, shiny, apicomedial boss, coarsely and irregularly punctate lateral to boss with punctures separated mostly by half a puncture width, surface shiny, unshagreened or delicately so; supraclypeal area coarsely punctate, shiny; vertex with lateral area punctures minute, separated mostly by 3 or 4 puncture widths; maxillary palpal ratio about 3.0:2.7:2.0:1.0. Thoracic sculpturing as in *coreopsis* but posteromedial mesoscutal punctures sparse, separated mostly by one to three puncture widths and with a small impunctate area, surface shiny, rarely shagreened. Abdomen as in *coreopsis* except as follows: tergum 1 with basal area punctures extremely small and shallow, separated mostly by one to three puncture widths; tergum 2 with basal area punctures separated by more than one puncture width and often by two or more widths, interband zone impunctate or with sparse punctures of irregular size, apical area impunctate, surface dulled by fine reticulotransverse shagreening except shiny basal area; tergum 3 similar but interband zone punctures more abundant; pygidial plate V-shaped, side slightly concave to slightly convex, slightly broader at base than median length, apex rounded.

Hair: Head white, often with sparse brown on vertex. Thorax pale ochraceous above, white on sides, scutellum brown medially, mesoscutum with brown posteromedian patch not much larger than scutellar brown patch, if any. Metasomal tergum 1 with basal

hairs white; tergum 2 with basal and distal pubescent bands white and broadly connected at sides, interband zone with short suberect brown hairs but these sparse, distal band not reaching apex, scarcely notched medially, thick, apical area glabrous or with sparse, subappressed, short, simple, brown hairs; tergum 3 similar but basal tomentum brown, apical area with more abundant brown; tergum 4 with apical white band uninterrupted; terga 5 and 6 dark brown, without lateral pale tufts; sterna dark brown. Legs white except as follows: basitibial plates, inner surfaces basitarsi (including hind), outer surfaces fore basitarsi, and often distitarsi dark reddish brown.

Male. Measurements and ratios: N, 20; length, 9-12 mm.; width, 2.5-4.0 mm.; wing length, M = 3.56 ± 0.239 mm.; hooks in hamulus, M = 12.10 ± 0.204; flagellar segment 2/segment 1, 9.55 ± 0.249.

Structure and color: Integument black except as follows: eyes greenish to bluish gray; apical half of mandible and distitarsi rufescent; flagellum reddish yellow to yellow beneath except first segment often all reddish brown and black above; wing membranes as in female, veins dark red to reddish brown; metasomal terga with hyaline, colorless apices, rarely slightly yellowed, often somewhat rufescent basal to hyaline areas; tegulae piceous; tibial spurs white.

Clypeus as in female but narrower, strongly converging towards mandibles, boss often less distinct; first flagellar segment with minimum length usually at least two-thirds maximum length and usually about equal to one-tenth maximum length of second segment, penultimate segment longer than three times minimum width, flagellum in repose reaching apex of marginal cell or almost; maxillary palpal ratio about 4.5:3.5:3.0:1.0. Sculpturing as in female except as follows: clypeal punctures smaller; mesoscutal punctures larger and usually more crowded posteromedially; tergum 1 with basal three to four-fifths punctate; tergum 2 with basal area punctures larger, separated mostly by one puncture width or less; terga 2, 3 and 4 with distinct round interband zone punctures. Terminalia as in *M. agilis* but gonostylus elbowed near base and median plate of sternum 7 with inner margin sinuate, not with distinct angle below (Figs. 86-89).

Hair: White except often extremely pale ochraceous on dorsum of thorax and vertex of head; thorax and head without brown; metasomal terga without brown except occasionally at extreme base of terga 3-6; tergum 2 with interband zone with bristlelike hairs

suberect and long, distal pubescent band thick, as long or longer than apical area medially; terga 2-4 with apical areas glabrous or with subappressed, simple white hairs; tergum 1 with thick, appressed, white, apical pubescence only in lateral fourths, long basal hairs subappressed near apex and reaching or surpassing apex medially unless worn; inner surfaces hind basitarsi yellow.

Bionomics. This species is widely distributed in southwestern United States and Mexico. From the collection data available, *M. tristis* seems to have three generations per year in Texas, New Mexico and Arizona. It probably has fewer than three to the north and perhaps more than three to the south of this area. The first peak of abundance in the southern Texas-Arizona area occurs in the

TABLE IX. Summary of Floral Records for *Melissodes tristis.*

Plant Data			Records of *M. tristis*			
FAMILY	Number of genera	Number of species	Number of collections	Number of females	Number of males	Total number of bees
Leguminosae: *Melilotus* spp.	1	2	27	88	181	269
Medicago sp.	1	1	23	31	8	39
Larrea spp.	1	2	11	104	0	104
Other genera	11	15	22	68	25	93
Compositae: *Gaillardia* spp.	1	3	28	53	36	89
Helianthus spp.	1	3	26	18	62	80
Aster spp.	1	3	13	11	3	14
Other genera	26	34	67	76	107	183
Malvaceae	4	9	57	198	31	229
Cactaceae	1	4	20	37	9	46
Hydrophyllaceae	1	2	9	54	9	63
Brassicaceae	5	6	19	31	18	49
Other families (29)	39	47	105	145	253	398
Totals	93	131	424	881	750	1,631

latter part of April and the first half of May. The second and the greatest peak of abundance occurs in early to middle July. The third and least peak occurs in the first half of September.

A species of *Melissodes* which has several generations per year and which can thus be found visiting flowers from early March until early November, can be assumed to be polylectic to a certain degree. This is true of *tristis*. It is the most polylectic of all of the species of the subgenus *Eumelissodes*. It seems to prefer plants of the families Leguminosae, Compositae and Malvaceae in that order. Thus, *M. tristis* is one of the few *Eumelissodes* which does not show a strong predilection for composites as pollen sources. On the contrary, the collection data indicate that composites should be placed third as sources of pollen, if the ratio of females to males is indicative of such a preference, as the author assumes it to be. The available floral data for *M. tristis* are summarized below in Table IX. Note the great variety of plants visited as shown by the numbers of families, genera and species.

Type Material. Holotype male of *tristis* from Las Cruces, New Mexico, August 2, is in the collection of the Academy of Natural Sciences of Philadelphia, Pennsylvania. Lectotype female, here designated, of *pallidicincta*, from West Fork Gila River, New Mexico, July 16, is in the collection of the U. S. National Museum, Washington, D. C. (USNM No. 3357). Holotype male of *tristis malvina* from Cerro Chilicota, Chihuahua, Mexico, March 22, C. H. T. Townsend, is in the collection of the Museum of Natural History, University of Colorado, Boulder. Holotype male of *semitristis* from Oak Creek Canyon, Arizona, July, F. H. Snow, is in the Snow Entomological Museum, University of Kansas, Lawrence. Holotype female of *pallidicincta erythrina* from Colorado Springs, Colorado, June 15-30, 1896, H. F. Wickham, is in the collection of the American Museum of Natural History, New York City.

Distribution. M. tristis ranges from Nebraska, Colorado, Utah, Nevada, and California, south to southcentral Mexico (Fig. 19). It has been collected from March 14 to November 4, but chiefly in early July. A total of 1,707 females and 1,673 males have been examined from the localities recorded below. Published records are included only when verified by the author.

ARIZONA: Amado; Apache Junction; Aquila; Arivaca; Ashfork; Benson; Bill Williams' Fork; Bisbee; Bonita (Stewart Lake); Bowie; Cameron; Camp Verde (5 miles S. E.); Canelo; Carr Canyon, Huachuca Mts.; Carr Peak, Cochise Co.; Carrizo Creek; Casa

Grande; Catman (Cat Mt.?); Cave Creek, Chiricahua Mts.; Chambers (3 miles W.); Chandler; Chino Valley; Cochise Co.; Continental; Cornville; Dewey; Dona; Douglas; Drake (4 miles N.); Duncan; Duquesne; Elfrida; Elroy; Fish Creek, Tonto National Forest; Flagstaff; Fort Huachuca; Gila Bend (25 miles E.); Globe; Graham Mts.; Grand Canyon; Granite Dells; Gray Mt. (10 miles W.), Coconino Co.; Groom Creek; Harshaw; Holbrook; Jerome;

FIG. 19. Map showing the known distribution of *M. (Eumelissodes) tristis* Cockerell.

Kansas Settlement; Kayenta; Kingman; Kirkland (Peeples Valley); Lochiel; Madera Canyon, Santa Rita Mts.; Marana; McNeal; Mesa; Millers Canyon, Huachuca Mts.; Mt. Lemmon (Molino Basin); Mt. View (6 miles S.); Nicks, Huachuca Mts.; Oak Creek Canyon; Onion Saddle, Chiricahua Mts.; Oracle; Painted Canyon Ranch, Chiricahua Mts.; Paradise, Chiricahua Mts.; Patagonia Mts.; Payson; Peach Springs; Pearce; Petrified Forest; Phoenix; Picacho; Pima (3 miles S.); Pinal Mts.; Portal (5 miles W. at S. W. Research Station); Prescott; Ramsey Canyon, Huachuca Mts.; Roosevelt Lake; Rustlers Park, Chiricahua Mts.; Safford; Saint David; Salt River Bridge (near Seneca); San Bernardino Valley, Chiricahua Mts.; San Francisco Mts.; San Simon; Santa Catalina Mts.; Sedona; Seligman; Seneca (10 miles S.); Seven Springs, Maricopa Co.; Show Low (14 miles S.); Skull Valley, Yavapai Co.; Snowflake, Navajo Co.; Sonoita; Springerville (25 miles N.); Stanfield (10 miles W.); Stewart Ranch (24 miles N. W. Prescott); Stockton Pass, Pinaleno Mts.; Superior (Boyce Thompson Arbor); Supai, Havaisu Canyon; Toltec; Tombstone; Tucson; Vernon; Warren; Weaver Mts., Yavapai Co.; White Mts.; Whiteriver; Willcox; Williams; Winslow. California: Naples; Riverside. Colorado: Antonito; Bellevue; Boulder; Canon City; Colorado Springs; Cotopaxi; Crowley; Denver; Elberta; Florissant; Fort Collins; Fountain; Greeley; Holly; Julesburg; La Junta; Lamar; Las Animas; Mesa Verde; Mischawauka; Nederland; Pagosa Springs; Pingree Park; Portland; Poudre Canyon (near Fort Collins); Prowers; Pueblo; Rock Creek, Routt Co.; Rocky Ford; Salida; Starkville; Steamboat Springs; Sterling; Trinidad; Westcliff. Kansas: Clark Co.; Coolidge (S. of); Garden City (7 miles E. and 10 miles W.); Greeley Co.; Hamilton Co.; Hugoton (4 miles S. E.); Johnson (2 miles N.); Morton Co.; Rexford; Syracuse (10 miles E.); Wallace Co. Louisiana: New Orleans. Nebraska: Mitchell. Nevada: Austin; Baker (Snake Valley), White Pine Co.; Eureka; Tonopah. New Mexico: Acme; Alamogordo; Albuquerque; Albiquie (15 miles N. W.); Artesia; Buckhorn; Carlsbad; Carrizozo; Cedro Canyon, Bernalillo Co.; Cienega Canyon, Sandia Mts.; Clifton House, Colfax Co.; Cloudcroft; Columbus (10 miles N.); Corona; Cuba (32 miles N. W. and 36 miles N.); Cuervo; Datil; Deming; Dripping Spring, Organ Mts.; Eddy Co.; Elda; Embudo; Endee, Quay Co.; Filmore Canyon; Frijolitos Canyon, Sandoval Co.; Gallup; Garfield; Gila River (West Fork); Glenwood; Hatch; Hot Springs; Hurley (5 miles S.); Isleta; Jemez Mts.; Juan Tabo area, Sandia Mts.; La Jara (5 miles E.); Las Cruces; Las Vegas; Lordsburg; Lov-

ing; Luna Co.; Madrid; Magdelena Mts.; Malaga; Maxwell; Mescalero; Mesilla Park; Montoya; Moriarty; Moses; Mountain Park; Nogal; Pecos; Portales; Quemado; Questa; Radium Springs; Raton; Red Hill (25 miles N. of Quemado); Rodeo; Roswell; Rowe; San Jon; San Jose; San Marciel; Santa Fe; Sapello; Silver City; Springer; State College, Dona Ana Co.; Steins; Tecolote; Tularosa; Vaughn; Whites City; White Sands; Winslow. TEXAS: Abilene; Alfred; Alpine; Amarillo; Austin; Bakersfield; Balmorhea; Bexar Co.; Big Bend National Park; Boragia; Brazos Co.; Brewster Co.; Bronco; Brownsville; Cherry Spring; Chisos Mts., Brewster Co.; Christoval; Comfort; Comstock; Concan (8 miles S.); Cornudas; Cotulla; Crane; Davis Mts.; Dell City (9 miles S.); Del Rio (23 miles S.); Devils River; Eagle Pass; Edinburg; El Paso; Fedor, Lee Co.; Finlay; Fort Davis; Fort Stockton; Harper; Hereford (5 miles S. W.); Hueco; Imperial; Kerrville; Lobo, Culberson Co.; Marathon; Marfa; Mason (10 miles N.); Maverick Co.; Mission (15 miles N. W.); Nueces River, Zavalla Co.; Odessa; Pecos; Pecos River; Presidio Co.; Quemado; Reeves Co.; Rio Grande, Brewster Co.; Sabinal; San Antonio; Sanderson; Santa Elena Canyon, Big Bend National Park; Shumla, Val Verde Co.; Sierra Blanca; Sonora; Stonewall; Toyah; Uvalde; Valentine; Van Horn; Westbrook; White Horse Plateau, Culberson Co.; White Rose Canyon, Jeff Davis Co. UTAH: Beaver; Bluff; Bryce Canyon; Delta; Dove Creek; Erda; Jericho; Iosepa; Jensen (12 miles E.); Juab; Kanab; Kanarraville; Monticello; Moxlena; Oak City; Petersboro; Promontory; Salt Lake City; Santa Clara; Skull Valley; South Cove Fork; Tooele; Vernal. WYOMING: Cheyenne. *México.* AGUASCALIENTES: Aguascalientes; El Retono (10 miles E. of Aguascalientes); Rincon de Romos (12 km. N.). CHIHUAHUA: Agua Caliente, Santa Barbara District; Camargo (20 miles S. W.); Catarinas; Cerro Chilicothe; Charcos, Allende District; Chihuahua; Ciudad Juaréz (87 km. S.); Delicias; Jiménez; Matachic; Moctezuma; Ojo Laguna; Parrál; Parrita; Salaíces; Samalayuca; San Jose Babicora; San Pablo Balleza; Santa Barbara; Santa Clara. COAHUILA: Guadalupe; La Rosa; Paila; Saltillo; San Pedro de las Colonias. DURANGO: Durango; El Tascate; Encino; Laguna District; La Loma; Nombre de Dios; Otinapas; Palos Colorados; Pedricena; San Juan del Río; Santa Maria del Oro; Villa Ocampo; Yerbanis, Cuencame District. HIDALGO: Actopán; Ismiquilpan. JALISCO: Encarnacion de Diaz; Lagos de Moreno (15 miles N. E.); Ojuelos; San Juan Lagos. NUEVO LEON: Monterey; Vallecillo. PUEBLA: Puebla (6 miles S. W.); Tehuacán. QUERETARO: San Juan del Río

(5 miles E.). San Luis Potosí: Huizache. Tamaulipas: Llera. Zacatecas: Fresnillo; Guadalupe; Sain Alto; Sombrerete (15 km. E.).

Flower Records. Acacia sp., *Actinea* sp., *A. acaulis, A. richardsonii, Allionia incarnata, Arabis* sp., *Argemone* sp., *Asclepias* sp., *A. galloides, A. verticillata, Aster* sp., *A. canescens, A. spinosa, A. tenacetifolium, Astragulus* sp., *Baccharis* sp., *Bahia sp., Baileya multiradiata, Berberis trifoliata, B. wilcoxii, Canotia holacantha, Ceanothus* sp., *C. fendleri, C. greggii, Celtis pallida, Cercidium* sp., *C. texanum, Cevalia sinuata, Chilopsis* sp., *C. linearis, C. saligua, Chrysopsis hispida, Chrysothamnus* sp., *Cirsium* sp., *C. ochrocentrum, C. undulatum, Cleome* sp., *C. luteum, C. serrulata, Convolvulus* sp., *Croton* sp., *C. luteovirens, Dalea lasianthera, Dasylirion wheeleri, Encelia* sp., *Engelmannia pinnatifida, Erigeron* sp., *E. canadensis, Eriogonum* sp., *E. trichopos, Euphorbia albimarginata, Eyesenhardtia polystachya, E. spinosa, Gaillardia* sp., *G. pinnatifida, G. pulchella, G. suavis, Gaura* sp., *Gilia calcarea, Gossypium herbaceum, Grindelia* sp., *Gutierrezia* sp., *G. californica, Haplopappus* sp., *H. gracilis, H. laricifolius, Helenium autumnalis, H. hoopesii, H. laciniatum, Helianthus* sp., *H. annuus, H. ciliaris, H. petiolaris, Hoffmanseggia densiflora, H. jamesii, Hymenothrix wislizeni, Iris mios, Kallstroemia* sp., *K. grandiflora, Larrea* sp., *L. divaricata, L. tridentata, Lepidium* sp., *Lesquerella* sp., *L. ovalifolia, Lippia cuneifolia, L. ligustrina, Lotus* sp., *Lupina* sp., *Lygodesmia juncea, Malvastrum cockerelli, Marrubium vulgare, Medicago sativa, Melilotus* sp., *M. alba, M. officinalis, Mentzelia multiflora, Mertenzia franciscana, Mimosa borealis, Monarda* sp., *M. citriodora, M. pectinata, Mortonia scabrella, Nepeta cataria, Nolina* sp., *N. microcarpa, Opuntia* sp., *O. basilaris, O. lindheimeri, O. macrorhiza, Parkinsonia* sp., *Pectis papposa, Penstemon superba, Petalostenum* sp., *P. candidum, P. flavescens, P. occidentatum, Phacelia* sp., *P. glandulosa, P. popei, Philadelphus microphyllus, Polemonium* sp., *Prionopsis* sp., *Prosopis* sp., *P. juliflora, Psoralea tenuiflora, Pyracantha* sp., *Ratibida* sp., *R. columnaris, R. tagetes, Rhus* sp., *Rosa* sp., *Salix* sp., *Salsola kali, S. pestifer, Salvia lemmoni, Sapindus drummondii, S. sapinarius, Senecio longilobus, S. werneriaefolius, Solanum elaeagnifolium, Solidago annua, S. stenolobus, Sphaeralcea* sp., *S. angustifolia, S. coccinea, S. emoryi, S. laxa, S. lobata, S. marginata, Stephanomeria* sp., *Tamarix* sp., *T. gallica, Thurberia thespesioides, Verbena stricta, Verbesina encelioides, Vernonia* sp.,

Vicia sp., *Wislizenia refracta, Zexmenia podocephala, Zinnia grandiflora.*

Melissodes (Eumelissodes) boltoniae Robertson

Melissodes boltoniae Robertson, 1905, Trans. Amer. Ent. Soc., vol. 31, p. 368; Cockerell, 1907, Ann. Mag. Nat. Hist., ser. 7, vol. 20, p. 127; 1909, Ann. Mag. Nat. Hist., ser. 8, vol. 4, p. 26; Robertson, 1914, Ent. News, vol. 25, p. 70; 1926, Ecology, vol. 7, p. 379; 1928, Flowers and Insects, p. 8; Pearson, 1933, Ecol. Monogr., vol. 3, p. 380; Brimley, 1938, Insects of North Carolina, p. 462.

Melissodes melandri Cockerell, 1906, Trans. Amer. Ent. Soc., vol. 32, p. 109 (new synonymy).

M. boltoniae is a small species related to *M. coreopsis*. It can be distinguished from *coreopsis* by the coarsely punctate tergal apices, especially in the female, the often infumate to piceous tergal apices of the male, the often tessellate galeae of both sexes, and the generally darker vestiture of both sexes.

Female. Measurements and ratios: N, 20; length, 10-12 mm.; width, 3.5-4.5 mm.; wing length, M = 2.89 ± 0.163 mm.; hooks in hamulus, M = 11.45 ± 0.145; flagellar segment 1/segment 2, M = 1.85 ± 0.026.

Structure and color: Integumental color as in *coreopsis* except as follows: flagellum darker, second segment never pale beneath, segments 3 to 10 dark reddish brown below; wing membranes colorless or slightly infumate; tergum 1 completely piceous or extremely narrowly hyaline apically, rufescent area, if present, less than one-fourth length of tergum.

Structure and sculpturing as in *coreopsis* except as follows: clypeal surface moderately shiny, somewhat dulled by cross-striations; supraclypeal area usually somewhat dulled by fine reticular shagreening; galeae usually dulled by reticular shagreening above at least in apical half; maxillary palpal ratio about 4:3:3:1, rarely with minute fifth segment present, often fourth segment slightly longer; second flagellar segment measured below as long as broad or almost so. Mesoscutum usually with small posteromedial impunctate area. Metasomal tergum 1 with basal half to three-fifths punctate, punctures large, round, deep, often same diameter as median scutellar punctures, separated mostly by one to two puncture widths, apical area impunctate and extended to form impunctate anterolateral lobes; tergum 2 with basal area punctures separated mostly by one to two puncture widths, surface often with fine reticular shagreening, apical area with abundant minute punctures two to three times diameter of hairs arising from them, extending to within one hair length of apical margins and separated mostly by two to four

puncture widths, sparser apically; tergum 3 similar to 2 but interband zone punctures crowded and apical area punctures more abundant, separated mostly by two to three puncture widths; tergum 4 like 2 but apical area absent or reduced to short, very broad, apical triangle with punctures separated mostly by one to two puncture widths.

Hair: As in *coreopsis* except as follows: pale hairs and pubescence white except occasionally pale ochraceous on anterior part of mesoscutum; more variable, some specimens almost entirely black. Palest specimens as in *coreopsis* except dark mesoscutal patch extending forward at least to a transverse line at anterior margins of tegulae, posterior pronotal lobes with at least a few black hairs mixed with the white, tergum 2 with distal pale band interrupted medially, tergum 4 with a few apicomedial, relatively simple, black hairs, sterna black to brown medially and white laterally, scopae white to ochraceous. Darkest specimens completely black except short white distal fasciae on terga 2 and 3, pale scopal hairs, tergum 1 ochraceous basally, and often a few white hairs on face near antennal fossae and on mesoscutum near tegulae. Thoracic hairs above long as in *coreopsis;* tergum 2 with interband zone hairs brown to black, suberect to subappressed, relatively simple, short; terga 2 and 3 with apical area hairs short, reaching or surpassing apical margins medially, black to brown, appressed to subappressed; scopal hairs as in *coreopsis.*

Male. Measurements and ratios: N, 20; length, 9-11 mm.; width, 2.5-3.5 mm.; wing length, $M = 2.74 \pm 0.194$ mm.; hooks in hamulus, $M = 10.85 \pm 0.196$; flagellar segment 2/segment 1, $M = 8.43 \pm 0.140$.

Structure and color: Integument black except as follows: clypeus yellow except brown to testaceous apical margin and dark tentorial pits; labrum often with small mediobasal pale spot; apical half of mandible and often distitarsi rufescent; eyes green to bluish green; flagellum below except first segment red and brown above; wing membranes clear to slightly infumate, veins reddish brown to black; tergal apices piceous, occasionally slightly translucent but then smoky brown.

Structure as in *coreopsis* except as follows: minimum length first flagellar segment equals more than one-tenth and usually less than one-eighth maximum length second segment, flagellum in repose reaching slightly beyond pterostigma; galeae usually dulled above at least in apical half; maxillary palpal ratio about 4.5:4.5:3.3:1.3:1.0, fifth segment often absent and then fourth segment slightly

longer. Sculpturing as in female except as follows: posteromedial impunctate mesoscutal area often reduced or absent; tergum 1 punctate in basal five-sixths or more, punctures usually more crowded; tergum 2 with interband zone punctures often larger and sparser; terga 2 and 3 with apical area punctures usually smaller and sparser. Terminalia much as in *M. agilis* (Figs. 84-85).

Hair: Palest specimens as in *coreopsis* except as follows: usually with at least a few brown hairs posteromedially on mesoscutum and medially on scutellum; vertex of head and tegulae often with brown; tergum 1 with simple, appressed to subappressed, long brown to black hairs in apical area usually reaching apical margin medially; tergum 2 with brown in interband zone and apical area; tergum 3 brown except distal pale pubescent band; terga 4 and 5 similar to 3; terga 6 and 7 golden brown to dark brown medially, paler laterally; sterna golden medially to white laterally. Darkest specimens have pale hairs and pubescence dark ochraceous to rust-colored but paler on lower parts of head and thorax; with abundant brown on vertex of head, tegulae, mesoscutum, scutellum; apical third of tergum 1 brown; terga 2 and 4 with distal pale bands interrupted medially, almost wholly brown on tergum 4 and wholly so on tergum 5; sterna brown medially to ochraceous laterally; legs ochraceous except inner hind basitarsi yellow.

Geographic Variation. Although the variation in color of vestiture is great in *M. boltoniae*, this varation does not appear to be distributed geographically so as to be able to recognize and name subspecific units. The darkest specimens are abundant in east-central Texas, but also occur in Illinois, Indiana, and Louisiana and pale specimens occur together with the dark even in Texas. Where, as in Texas, a reasonably long series of specimens are available, all intergrades occur between the darkest and the palest individuals.

Bionomics. All that can be said about the flower preferences of this bee at this time is that it is an oligolege upon plants of the family Compositae. Out of 40 collections (106 females and 97 males) for which flower data are available, 38 are from some composite and only two are from other families of plants (and these last involve only four males). Of the composites visited by *M. boltoniae* the following genera figure prominently: *Aster, Amphiachyris, Helianthus, Solidago*, and *Bidens*. In the vicinity of Lawrence, Kansas, *boltoniae* can almost invariably be found collecting pollen from flowers of *Amphiachyris dracunculoides*.

Type Material. Lectotype female, here designated, of *boltoniae*, collected by Charles A. Robertson, August 31, 1886, at Carlinville, Illinois, on *Coreopsis aristosa*, is in the collection of the Illinois Natural History Survey, Urbana, Illinois. Of the paratypes accompanying this lectotype several are *M. illata* (described below), rather than *M. boltoniae*. The holotype female of *melandri* (a melanistic female) from Fedor, Lee Co., Texas, October 4, 1899, is in the collection of Mr. P. H. Timberlake, Citrus Experiment Station, Riverside, California.

Distribution. *M. boltoniae* ranges from Minnesota south to eastern Texas and east to Ohio, North Carolina, and Florida (Fig. 20). It has been collected from July 17 to November 6, but chiefly

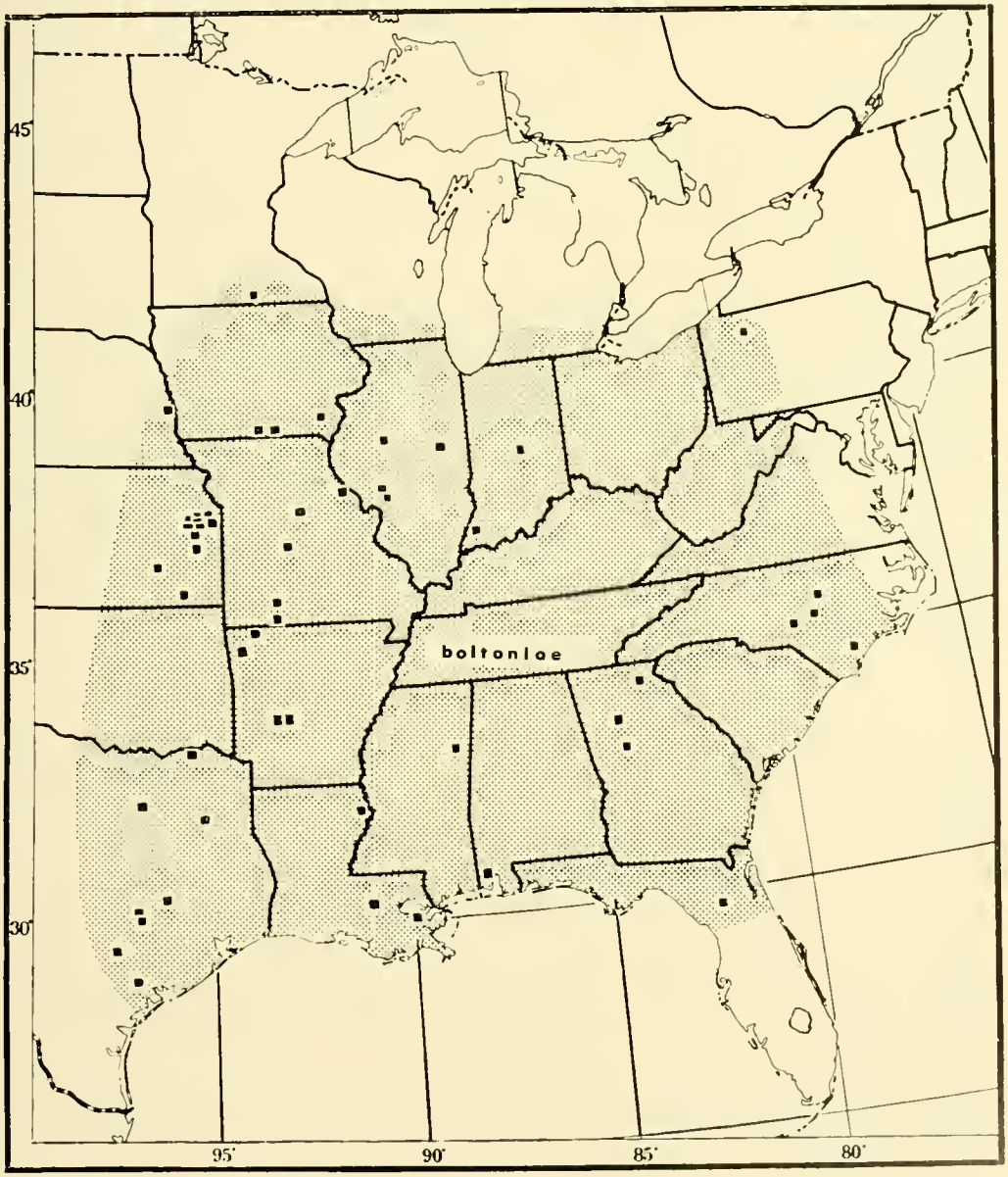


FIG. 20. Map showing the known distribution of *M. (Eumelissodes) boltoniae* Robertson.

in late August and September. In addition to the type material, 162 females and 148 males have been examined from the localities listed below (published records are included only when verified by the author).

ALABAMA: Kushla. ARKANSAS: Eureka Springs; Fayetteville; Hot Springs; Knob Hill Reservation, Ouachita Mts. FLORIDA: Gainesville. GEORGIA: Atlanta; Griffin; Mt. Yonah. ILLINOIS: Carlinville; Macoupin Co.; Manito; Urbana. INDIANA: Oaklandon; Rush Branch. IOWA: Appanoose Co.; Mt. Pleasant (6 miles S. W.); Wayne Co. KANSAS: Baldwin City; De Soto, Johnson Co.; Douglas Co.; Garnett; Independence (3 miles E.); Lawrence; Lone Star Lake, Douglas Co.; Olathe; Ottawa; Reece. LOUISIANA: Baton Rouge; Chalmette National Historical Park, Orleans Co.; Tallulah. MINNESOTA: Freeborn Co. MISSISSIPPI: West Point. MISSOURI: Branson; Columbia; Louisiana; Ozark; Ozark Lake. NEBRASKA: Omaha. NORTH CAROLINA: Burgaw; Harnett Co.; Southern Pines; Wake Co.; Washington Co. PENNSYLVANIA: Lynch, Forest Co. TEXAS: Brazos Co.; Chicota; Dallas, Fedor, Lee Co.; Palmetto State Park, Gonzales Co.; Tyler (3.5 miles N. W.); Victoria.

Flower Records. *Abutilon avicennae*, *Amphiachyris* sp., *A. dracunculoides*, *Aster* sp., *A. ericoides villosus*, *A. multiflorus*, *A. novaeangliae*, *A. praeatus*, *Bidens* sp., *B. involucrata*, *Boltonia asteroides*, *Cassia* sp., *Chrysopsis* sp., *Cirsium* sp., *Coreopsis aristosa*, *Helenium altissimum*, *H. autumnale*, *H. tenuifolium*, *Helianthus* sp., *H. annuus*, *H. grosse-serratus*, *H. tuberosus*, *Heterotheca latifolia*, *Lythrum* sp., *Ratibida pinnata*, *Rudbeckia triloba*, *Silphium* sp., *Solidago* sp., S. *canadensis*, S. *missouriensis*, *Verbena* sp., *V. stricta*, *Vernonia* sp., *V. baldwini interior*.

Melissodes (Eumelissodes) fumosa, n. sp.

This species is closely allied to *M. boltoniae*. The females of *fumosa* can be readily separated from those of *boltoniae* by the shorter second flagellar segment, the shorter mesoscutal and scutellar hairs, and the less punctate apical area of tergum two. The males of *fumosa* are separated from those of *boltoniae* only with great difficulty and uncertainty. The males of *fumosa* have the apical areas of the terga translucent, yellowish brown to almost colorless, and usually have a slightly shorter first flagellar segment, but *boltoniae* males overlap in both respects to some degree.

Female. Measurements and ratios: N, 20; length, 8-10 mm.; width, 3-4 mm.; wing length, $M = 2.54 \pm 0.084$ mm.; hooks in

hamulus, M = 10.95 ± 0.135; flagellar segment 1/segment 2, M = 1.82 ± 0.032.

Structure and color: Integument black except as follows: apical half of mandible and distitarsi rufescent; flagellar segments 3-10 dark red below; eyes gray to slightly green; wing membranes clear or slightly milky, veins dark brown to black; tegulae piceous; tibial spurs white; apex of tergum 1 extremely narrowly hyaline.

Clypeus as in *coreopsis* but surface shiny, with only slight striations, with apicomedian carina distinct; supraclypeal area moderately shiny, usually with fine reticular shagreening; lateral areas of vertex with minute punctures separated by one to three puncture widths, surface shiny; galeae dulled above by fine tessellation at least in apical half; maxillary palpal ratio about 7:5:5:2:1, fifth usually absent; second flagellar segment distinctly shorter than broad, usually length to width about 8:10 or 9:10. Mesosomal sculpturing as in *boltoniae.* Metasomal sculpture as in *boltoniae* except as follows: tergum 1 with basal three-fifths with punctures slightly smaller than scutellar punctures and separated mostly by half to two puncture widths medially; tergum 2 with basal area punctures separated mostly by half to one puncture width, surface unshagreened, interband zone punctures small, separated mostly by half to two puncture widths, apical area largely impunctate but with distinct punctures in basal half medially and almost to apical margin at sides; tergum 3 similar but interband zone and apical area punctures more abundant; terga 2 and 3 with apical areas shiny, shagreening extremely fine. Pygidial plate V-shaped, width subequal to length, apex rounded.

Hair: As in *boltoniae* except as follows: no tendency towards melanism; pale hairs of upper parts of thorax and head bright ochraceous; hairs of mesoscutum and scutellum short; posterior lobes of pronotum without dark hairs; tergum 2 with distal pale band narrowly interrupted medially; tergum 3 with pale band uninterrupted; tergum 4 with pale apical band without apicomedial notch; terga 5 and 6 usually without (holotype) pale lateral tufts; sterna with few or no pale laterally, all reddish brown.

Male. Measurements and ratios: N, 20; length, 8-9 mm.; width, 2.5-3.0 mm.; wing length, M = 2.52 ± 0.126 mm.; hooks in hamulus, M = 9.95 ± 0.170; flagellar segment 2/segment 1, M = 8.92 ± 0.223.

Structure and color: Integument black except as follows: clypeus light yellow except testaceous to red apical margin and ten-

torial pits; labrum black; apical half of mandible and distitarsi rufescent; flagellum yellow below, dark above, first segment usually all brown; eyes bluish gray to green; wing membranes colorless, veins reddish brown; tergal apices translucent, infumate, yellow brown to brown, never completely opaque.

Structure as in *boltoniae* except as follows: minimum length first flagellar segment usually equals one-tenth or less maximum length second segment; maxillary palpal ratio about 3.5:3.0:3.0:1.0, minute fifth occasionally present. Sculpturing as in *boltoniae* but tergum 1 with punctures often smaller and terga 2 and 3 with apical areas impunctate. Terminalia as in *agilis* (Figs. 90-91).

Hair: Vestiture as in *boltoniae* except as follows: pale hair of head and thorax often dull ochraceous; mesoscutum and tegulae often without dark hairs; tergum 2 with distal pale band usually narrow and occasionally interrupted medially; tergum 5 with distal pubescent band usually reaching apical margin across entire tergum; terga 6 and 7 with golden brown to dark reddish brown hair.

Type Material. Holotype female from Hattiesburg, Mississippi, collected by C. D. Michener, October 10, 1943, on *Chrysopsis microcephala,* and the allotype male from the same locale, collected by C. D. Michener, September 24, 1943, are in the collection of the Snow Entomological Museum of the University of Kansas, Lawrence, Kansas. Eleven female paratypes collected by C. D. Michener at Hattiesburg, Mississippi, are as follows: 2 females with the holotype; 3 females, September 26, 1943; 1 female, October 10, 1943; 1 female, October 17, 1944; 1 female, October 10, 1943, on *Aster dumosus;* 1 female, October 24, 1943, on *A. dumosus*; 2 females, October 1, 1944. One female paratype was collected by C. D. Michener at Camp Shelby near Hattiesburg on October 3, 1944. One male paratype was collected by F. C. Bishopp at West Point, Mississippi, September 16, 1904. The paratypes are in the Snow Entomological Museum, the U. S. National Museum, Washington, D. C., the collection of P. H. Timberlake, Citrus Experiment Station, Riverside, California, the American Museum of Natural History, New York City, and the author's personal collection.

Distribution. This species ranges from Maryland west to Nebraska and south to Mississippi and Alabama (Fig. 21). It has been collected from June 8 to October 24, but mainly in August and September. In addition to the type material listed above, 43 females and 56 males have been examined from the localities listed below (the type localities are included).

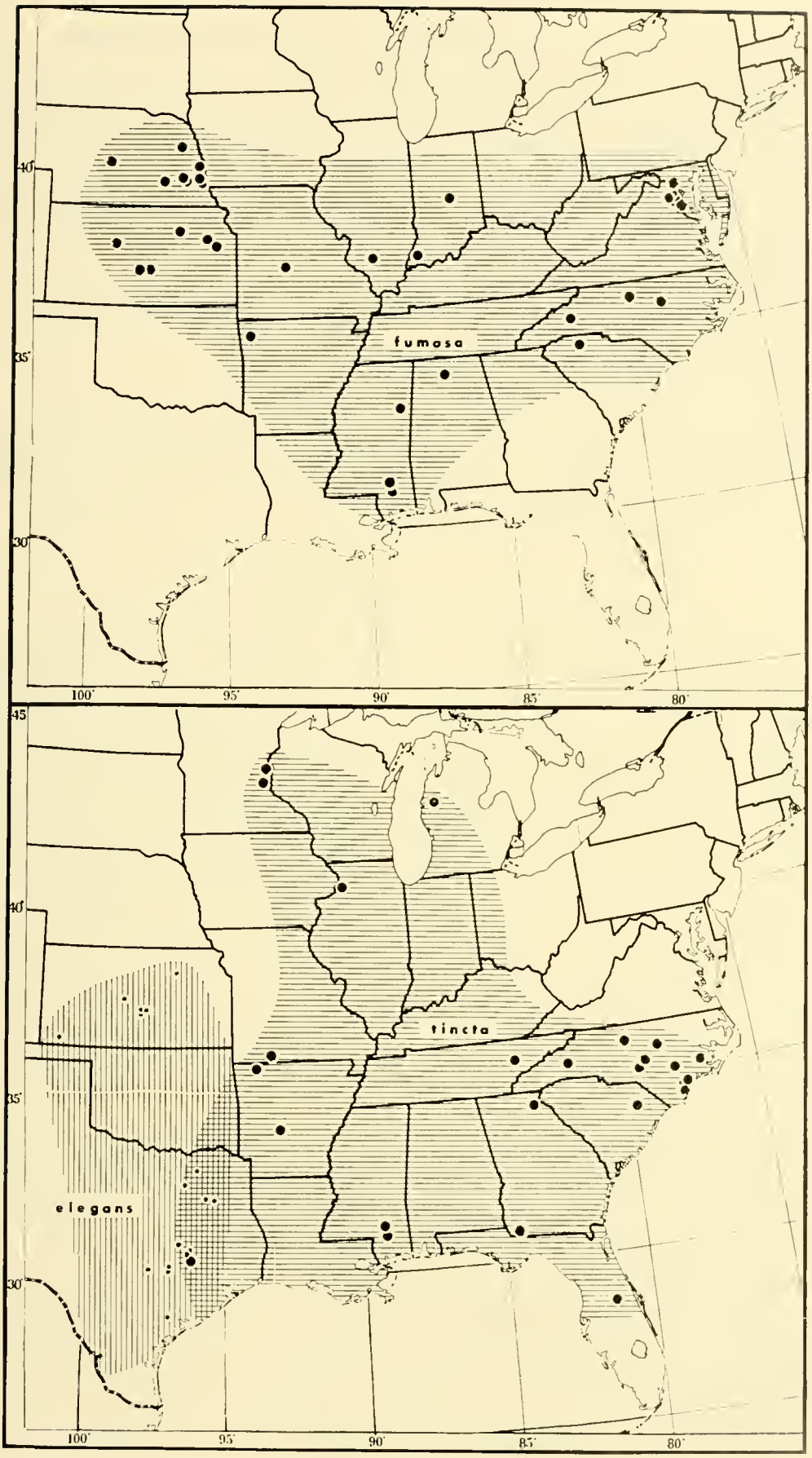


FIG. 21. Map showing the known distributions of *M. (Eumelissodes) fumosa* LaBerge, *M. (E.) elegans* LaBerge, and *M. (E.) tincta* LaBerge.

ALABAMA: Decatur. ARKANSAS: Fayetteville. ILLINOIS: Du Bois. INDIANA: Forest Reserve; Oaklandon; Rush Branch. KANSAS: Douglas Co.; Hays; Hutchinson (5 miles N. and 5 miles N. W.); Riley Co.; Topeka. MARYLAND: Cabin John; Indianhead. MISSISSIPPI: Camp Shelby; Hattiesburg; West Point. MISSOURI: Ozark Lake. NEBRASKA: Broken Bow; Lincoln; Louisville; Malcolm; Nebraska City; Omaha; West Point; York Co. NORTH CAROLINA: Greensboro; Marion; Raleigh; Umstead State Park. SOUTH CAROLINA: Spartanburg. VIRGINIA: Alexandria; Falls Church; Mount Vernon; Vienna.

Flower Records. *M. fumosa* is an oligolege of composites and seems to prefer flowers of the genus *Solidago*. *Asclepias tuberosus, Aster dumosus, Boltonia asteroides, Chrysopsis microcephala, Eupatorium linearifolium, Grindelia* sp., *Helenium* sp., *Koellia* sp., *Solidago* sp., *S. canadensis, S. glaberima, S. rupestris, S. serotina, Verbena* sp.

Melissodes (Eumelissodes) elegans, n. sp.

Melissodes elegans is very closely related both to *M. fumosa* and to *M. boltoniae*. The females are like the pale specimens of *boltoniae* in size and color, but can be distinguished by the smaller punctures on tergum 1, the more abundant and deeper punctures of the interband zone of tergum 2, the less punctate apical areas of terga 2 and 3, and the lack of dark hairs on the posterior pronotal lobes. The female can be distinguished from that of *fumosa* by the pale thoracic hairs being white, the coarse interband zone punctures of tergum 2, the less shiny apical areas of terga 2 and 3, and the larger size. The males are much more difficult to identify. They are similar to *fumosa* in the apical tergal areas being translucent, and they have the apical hairs of tergum 1 pale in color, often have pale labral spot, and occasionally have pale spots on the mandibular bases.

Female. Measurements and ratios: N, 20; length, 10-12 mm.; width, 3.5-4.5 mm.; wing length, $M = 2.90 \pm 0.100$ mm.; hooks in hamulus, $M = 12.15 \pm 0.182$; flagellar segment 1/segment 2, $M = 1.72 \pm 0.023$.

Structure and color: Integumental color as in *coreopsis* except as follows: second flagellar segment dark below; eyes dark gray (holotype) to bluish gray; wing membranes clear, veins dark reddish brown.

Structure and sculpture as in *coreopsis* with the following excep-

tions or additions: second flagellar segment distinctly longer than broad below (as in *boltoniae*); clypeal surface somewhat dulled by coarse cross-striations; lateral areas of vertex with minute punctures usually separated by two to three puncture widths; galeae dulled above by tessellation at least in apical half; maxillary palpal ratio about 3.5:3.5:3.0:1.0; posteromedial mesoscutal punctures large and sparse but not impunctate as in *boltoniae;* tergum 1 with basal area punctures separated by half to one puncture width and smaller than medial scutellar punctures, surface dulled by dense reticular shagreening; apical area impunctate but not usually with impunctate lobes extending anterolaterally; tergum 2 with basal area punctures round, deep, separated mostly by one puncture width or less, interband zone punctures round, deep, separated mostly by about one puncture width, apical area impunctate; tergum 3 similar to 2 but apical area with abundant minute punctures; pygidial plate with basal width subequal to length.

Hair: Vestiture color and form as in *boltoniae* except as follows: pale hairs white; no tendency towards melanism; posterior pronotal lobes and face without black hairs; mesoscutal dark patch usually extends forward to or beyond a transverse line at anterior margins of tegulae; tergum 1 with apical area with short simple brown hairs basally and extending in anterolateral lobes; tergum 2 with interband zone hairs black, simple, short, appressed to subappressed, with distal pale band usually uninterrupted medially, with apical area hairs abundant, simple, brown, appressed; tergum 4 rarely with short black fringe in median third (not in holotype); tergum 5 with pale lateral tufts, but not usually tergum 6.

Male. Measurements and ratios: N, 20; length, 8-11 mm.; width, 2.5-3.5 mm.; wing length, $M = 2.80 \pm 0.139$ mm.; hooks in hamulus, $M = 11.00 \pm 0.126$; flagellar segment 2/segment 1, $M = 8.77 \pm 0.284$.

Structure and color: Integumental color as in *fumosa* except as follows: labrum usually with mediobasal pale spot (allotype); mandibles occasionally with minute pale basal spots (not allotype); tergal apices translucent, infumate (allotype) to almost clear.

Structure and sculpture as in *fumosa* except as follows: minimum length first flagellar segment equals one-tenth or more of maximum length of second segment; maxillary palpal ratio about 7:6:6:2:1 (allotype), fifth often absent; galeae usually tessellate above at least in apical half; tergum 1 with minute punctures in apical area; tergum 2 with basal area and interband zone punctures

usually more abundant and surfaces shiny. Terminalia as in *agilis* but sternum 8 without apical hairs.

Hair: Vestiture as in *coreopsis* except as follows: pale hairs white to ochraceous; vertex without brown; mesoscutum with no (allotype) or few brown hairs; scutellum usually with a few median brown hairs; tergum 1 with apical area hairs short, subappressed, simple, yellow to white, surpassing apical margin; tergum 2 with interband zone hairs long, suberect, white, with apical area hairs subappressed, usually pale brown to black; tergum 3 with apical area hairs pale to dark brown; tergum 5 with distinct apical white band; terga 6 and 7 usually brown, occasionally golden brown.

Type Material. Holotype female, allotype male, and four paratype females, collected by L. H. Shinners, 3.5 miles N. W. of Tyler, Texas, October 12, 1952, on *Heterotheca latifolia* are in the collection of the Snow Entomological Museum of the University of Kansas at Lawrence. Nineteen female and thirteen male paratypes from Brazos Co., Texas, were collected by A. H. Alex as follows: 1 male, September 24, 1954, on *Eupatorium serotinum;* 1 male, September 30, 1954, on *Solidago serotina;* 3 males, October 4, 1954, on S. *serotina;* 1 male, October 5, 1954, on S. *serotina;* 1 female, 2 males, October 6, 1954, on S. *serotina*; 2 males, October 17, 1954, on *Helenium tenuifolium*; 1 female, October 24, 1954, on *Aplopappus divaricatus*; 1 male, October 24, 1954, on *Heterotheca subaxillaris;* 2 females, October 24, 1954, on *H. tenuifolium;* 2 females, October 31, 1954, on *H. subaxillaris;* 2 females, November 5, 1954, on *H. subaxillaris;* 6 females, November 12, 1954, on *H. subaxillaris;* 1 male, September 23, 1955, on *Verbesina encelioides;* 2 females, October 16, 1955, on *H. subaxillaris.* Paratypes are in the collections of Texas A. and M. College, College Station, Texas, the Snow Entomological Museum, the U. S. National Museum, Washington, D. C., and in the author's personal collection.

Distribution. This species is known only from Kansas and Texas (Fig. 21). It has been collected from August 26 to November 12, but chiefly in September and October. In addition to the type material, 23 females and 44 males have been studied from the localities listed below (this list includes the type localities).

KANSAS: Great Bend; Hugoton (4 miles S. E.); Hutchinson (3 mile W., 5 miles N., and 5 miles N. W.); Riley Co. TEXAS: Austin; Brazos Co.; Calvert; College Station; Dallas; Fedor, Lee Co.; Laredo; Lee Co.; Tyler (3.5 miles N. W.); Victoria, Wolfe City.

Flower Records. *M. elegans* has been collected on flowers other than composites only twice. Flower records are as follows: *Aplopappus divaricatus, Aster* sp., *Boltonia asteroides, Cleome* sp., *Croton monanthrogynus, Fagopyrum* sp., *Grindelia* sp., *Helenium tenuifolium, Heterotheca latifolia, H. subaxillaris, Polygonum* sp., *Prionopsis* sp., *P. ciliata, Solidago serotina, Verbesina encelioides.*

Melissodes (Eumelissodes) tincta, n. sp.

Melissodes tincta is a medium-sized bee related closely to *pilleata, elegans,* and *coreopsis.* The females of *tincta* are difficult to distinguish from the other species of this complex. They may be told from the females of *pilleata* and *coreopsis* by the finely tessellate or shagreened galeae in which they resemble *boltoniae* and *elegans.* They are larger than the females of *fumosa* and have the second flagellar segment longer. They can be distinguished from *boltoniae* females by the finer punctation of tergum 1 and the apices of terga 2 and 3, and from those of *elegans* by the generally darker color of the vestiture. The males are readily recognized by the usually opaque tergal apices and by the base of the clypeus being infumate with the pale apical yellow portion restricted to one- to two-thirds of the clypeus.

Female. Measurements and ratios: N, 20; length, 10-12 mm.; width, 3.5-5.0 mm.; wing length, M = 3.16 ± 0.138 mm.; hooks in hamulus, M = 12.30 ± 0.193; flagellar segment 1/segment 2, M = 1.75 ± 0.018.

Structure and color: Integumental color as in *coreopsis* except as follows: second flagellar segment black, segments 3-10 dark reddish brown to black below; eyes dark gray to gray or green; tergum 1 not rufescent in apical third, with extremely narrow hyaline margin.

Structure and sculpturing as in *coreopsis* except as follows: clypeus slightly protruding to flat, punctures small, separated by half a puncture width, surface dulled by striations or tessellation, apicomedian carina present, broad; supraclypeal area punctate, surface usually dulled by coarse shagreening; flattened areas of vertex with small punctures separated mostly by half to one puncture width, surface shiny; maxillary palpal ratio about 2.5:1.6:1.8:1.0; galeae dulled above by fine tessellation at least in apical half; mesoscutum with posteromedian area punctures sparse but not impunctate; tergum 1 with basal area punctures smaller than median scutellar punctures and separated mostly by one to two puncture widths, surface dulled

by fine reticulotransverse shagreening, apical area as in *elegans;* tergum 2 with basal area punctures separated mostly by less than one puncture width, interband zone punctures small, separated by a half to two puncture widths, apical area with minute punctures separated by three to four puncture widths and no more than twice basal width of hairs arising from them, surface as in *elegans;* tergum 3 like 2 but punctures more abundant and apical area punctures larger and more crowded; tergum 4 with apicomedian punctures present when dark apicomedian hairs are present (as in allotype); pygidial plate as in *coreopsis.*

Hair: Vestiture as in *coreopsis* except as follows: dark mesoscutal patch extends forward beyond a transverse line at anterior margins of tegulae; tegulae brown; posterior pronotal lobes usually black (in allotype) mixed with white; ventral parts of episterna usually brown; metasomal tergum 1 with apical area with short, closely appressed, brown hairs at least basad and in lateral lobes; tergum 2 with distal pale band interrupted medially, interband zone with short subappressed, and apical area with short appressed to appressed, dark brown hairs; tergum 3 with distal pale band uninterrupted and not reaching apical margin laterally; tergum 4 with apical fringe of dark hairs in median third (allotype) or more, occasionally black apical hairs absent, occasionally fringe expanded medially to form median triangular dark area; tergum 5 with few (allotype) or no lateral pale hairs; tergum 6 without lateral pale hairs; sterna dark brown, often pale laterally; legs as in *boltoniae.*

Male. Measurements and ratios: N, 10; length, 10-11 mm.; width, 3-4 mm.; wing length, $M = 3.27 \pm 0.158$ mm.; hooks in hamulus, $M = 11.90 \pm 0.233$; flagellar segment 2/segment 1, (5) $M = 9.19 \pm 0.298$.

Structure and color: Integument black except as follows: clypeus with apical margin testaceous, with apical transverse band of yellow one- to two-thirds length of clypeus; labrum cream-colored with dark border; apical half of mandible and tarsi rufescent; eyes yellowish gray to green; flagellar segments 3 to 11 red beneath, dark brown above; wing membranes hyaline, veins black to dark reddish brown; metasomal tergal apices piceous and opaque (holotype), rufescent, or rarely only slightly infumate.

Structure as in *coreopsis* except as follows: minimum length first flagellar segment equals one-eighth to one-tenth maximum length second segment, flagellum in repose reaching well beyond pterostigma but not beyond tip of submarginal cell; galeae usually dulled

above at least in apical half; maxillary palpal ratio about 3:2:2:1. Sculpturing as in *boltoniae* but terga 2 and 3 with apical area with sparse punctures. Terminalia as in *agilis* but sternum 8 with few or no hairs.

Hair: Head white with brown on vertex. Mesoscutum, tegulae, and scutellum with abundant reddish brown, thorax white on sides. Metasoma as in *boltoniae*.

Type Material. Holotype male from Camp Shelby (near Hattiesburg), Mississippi, collected by C. D. Michener, September 18, 1944, is in the Snow Entomological Museum, the University of Kansas, Lawrence. The allotype female from Hattiesburg, Mississippi, collected by C. D. Michener, October 10, 1943, on *Chrysopsis microcephala*, is in the collection of the American Museum of Natural History, New York City. Three female and six male paratypes collected by C. D. Michener are as follows: Hattiesburg: 1 female, September 24, 1944, on *Chrysopsis microcephala*; 1 male, September 24, 1944. Camp Shelby: 2 females, October 3, 1944; 1 male, October 14, 1944; 1 male, September 13, 1943; 2 males, September 23, 1944; 1 male with the holotype. Paratypes are in the Snow Entomological Museum, the American Museum of Natural History, the collection of P. H. Timberlake, Citrus Experiment Station, Riverside, California, and in the author's collection.

Distribution. This species is known from Minnesota and Michigan south to Texas and Florida (Fig. 21). It has been taken from August 6 to December 10, but chiefly in September and October. In addition to the type material, 51 females and 3 males have been examined from the localities listed below (this list includes the type localities).

Arkansas: Eureka Springs, Ouachita Mts.; Hot Springs. Florida: Conway; Larkins; South Miami. Georgia: Bainbridge; Clarkesville. Illinois: Fulton. Michigan: Lake Co.; McCarty Creek, Loon Lake, Lake Co. Minnesota: Lake Vadnais, Ramsey Co.; North Branch. Mississippi: Camp Shelby; Hattiesburg. Missouri: Branson. North Carolina: Burgaw; Cherry Point; Faison; Holly Shelter; Marion; Raleigh; Southern Pines; Wilmington; Yadkin Co. South Carolina: Florence. Tennessee: Knoxville. Texas: Ben Wheeler (3.7 miles S. E.); Brazos Co.

Flower Records. M. tincta is an oligolege of composites and seems to prefer the genera *Chrysopsis* and *Aster* in that order. *Aster* sp., *A. longicaulus, Chrysopsis* sp., *C. microcephala, Helianthus maximillianus, Verbesina encelioides.*

Melissodes (Eumelissodes) pullata Cresson

Melissodes pullata Cresson, 1865, Proc. Ent. Soc. Philadelphia, vol. 4, p. 189; Bray, 1917, Pomona Jour. Ent. Zool., vol. 9, p. 94 (probably misidentification).

M. pullata is a small dark Cuban species closely related to *M. boltoniae* of the mainland. The female is distinctive in that the scopal hairs are wholly or largely brown, the galeae are dulled by shagreening and the wings are deeply infumate. The males have piceous tergal apices, infumate wings and the distal pale band of tergum 2 interrupted medially.

Female. Measurements and ratios: N, 20; length, 9-10 mm.; width, 3.5-4.0 mm.; wing length, M = 3.05 ± 0.087 mm.; hooks in hamulus, M = 11.85 ± 0.174; flagellar segment 1/segment 2, M = 1.86 ± 0.051.

Structure and color: Integumental color as in *boltoniae* except as follows: flagellum dark brown to black below; eyes greenish gray to dark gray; wing membranes deeply infumate, brown, veins black.

Structure and sculpture as in *boltoniae* except as follows: clypeal surface dulled by coarse reticular shagreening; supraclypeal area moderately dulled by shagreening; galeae dulled above by fine tessellation; maxillary palpal ratio about 3.0:1.8:1.6:1.0; second flagellar segment slightly broader than long. Mesoscutum with posteromedian impunctate area extremely small, if present, usually with punctures in posteromedian area separated by one to two puncture widths, surface shiny, unshagreened or delicately so; mesepisterna with surfaces usually slightly dulled by extremely fine, irregular shagreening. Metasomal tergum 2 with basal area punctures separated mostly by a half puncture width, surface shiny, interband zone punctures regular, separated mostly by one puncture width or slightly more, surface moderately shiny, apical area with minute scattered punctures no larger than twice diameter of hairs arising from them; tergum 3 like 2 but apical area shorter and with fewer punctures, interband zone punctures crowded; tergum 4 like 3 but apical area reduced to small median triangular area; pygidial plate as broad at base as long or broader.

Hair: Head and thorax black. Abdomen black except as follows: distal pubescent band of tergum 2 often partly white, interrupted medially; pubescent bands of terga 2-4 all present but usually dark brown. Legs dark brown except scopal hairs of hind tibiae often dark ochraceous or light brown, especially apically.

Male. Measurements and ratios: N, 20; length, 9-11 mm.; width, 2.5-3.5 mm.; wing length, M = 3.03 ± 0.156 mm.; hooks in hamulus, M = 11.40 ± 0.279; flagellar segment 2/segment 1, (14) M = 9.46 ± 0.153.

Structure and color: Integumental color as in *boltoniae* except as follows: labrum without pale post; eyes gray to greenish gray; wing membranes infumate, yellowish brown, veins dark reddish brown to black; tergal apices piceous.

Structure as in *boltoniae* except as follows: maxillary palpal ratio about 3.5:2.2:2.0:1.0; flagellum in repose reaching well beyond pterostigma. Sculpture as in female except as follows: clypeal punctures indistinct; galeae often shiny above and without tessellation except in apical thirds; metasomal tergum 1 punctate to within one-sixth or one-seventh of apical margin but punctures in last fourth of punctate area progressively smaller and sparser; tergum 2 with apical area virtually impunctate; terga 3-5 similar to 2 but apical areas shorter. Terminalia as in *agilis.*

Hair: Head ochraceous usually with brown on vertex. Thorax ochraceous laterally; scutellum dark brown fringed with ochraceous; mesoscutum with dark brown posteromedian patch twice size of scutellar dark patch or larger; ochraceous elsewhere; tegulae with brown. Metasomal tergum 1 ochraceous basally, apical area and anterolateral lobes of apical area with abundant, dark brown, suberect to subappressed, simple hairs; tergum 2 white basally, distal pale band pale ochraceous, interrupted medially, lateral fasciae tapered mesad, interband zone with abundant dark brown, suberect, simple hairs; apical area with subappressed to suberect, dark brown, simple hairs; tergum 3 similar to 2 but basal tomentum brown, apical area subequal in length to distal pale band medially and distal band uninterrupted; tergum 4 like 3 but apical area shorter and distal pale band often brown medially; tergum 5 like 4 but distal pubescent band entirely brown; terga 6 and 7 brown; sterna brown medially to pale ochraceous laterally. Legs ochraceous except orange inner surfaces tarsi and often brown basitibial plates.

Type Material. Lectotype female of *pullata* from Cuba is in the collection of the Philadelphia Academy of Sciences (Type No. 2303), Philadelphia, Pennsylvania.

Distribution. M. pullata is known to occur only in Cuba. It has been collected from September 5 to September 30. In addition to the lectotype, 25 females and 25 males have been examined from the localities listed below.

CUBA: Cabanas, Piñar del Río; Cotorro, Havana; Loma del Gato (Sierra del Cobre), Oriente; Piñar del Río; Playa de Manauas, Havana; Viñales (7 and 24 kilometers N.).

Melissodes (Eumelissodes) persimilis Cockerell

Melissodes persimilis Cockerell, 1949, Proc. U. S. National Museum, vol. 98, p. 463.
Melissodes perplexans Cockerell, 1949, Proc. U. S. National Museum, vol. 98, p. 463 (new synonymy).
Melissodes griseihirta Cockerell, 1949, Proc. U. S. National Museum, vol. 98, p. 463 (new synonymy); Michener, 1954, Bull. Amer. Mus. Nat. Hist., vol. 104, p. 132.
Melissodes aurescens, Cockerell, 1949, Proc. U. S. National Museum, vol. 98, p. 462 (misidentification—see variety A).

This species is from Central America and is related to our more northern species *montana* and *confusa*. The female differs from that of *montana* by having no brown hair on the tegulae, little or no brown on the mesoscutum, and the distal pale band of tergum 2 being narrowly interrupted medially. The male has no brown hairs on tegulae, mesoscutum, or scutellum, and thus differs from *montana* and *confusa* and also the related *floris* of southern Mexico.

Female. Measurements and ratios: N, 3; length, about 12 mm.; width, about 4.5 mm.; wing length, M = 3.35 ±0.233 mm.; hooks in hamulus, M = 13.00 ± 0; flagellar segment 1/segment 2, M = 1.88 ± 0.099.

Structure and color: Integumental color as in *coreopsis* except as follows: eyes bluish gray; wing membranes colorless to slightly infumate, veins black; tegulae piceous.

Structure and sculpture as in *coreopsis* except as follows: clypeus with well-developed apicomedian carina, surface dulled by coarse reticular shagreening; supraclypeal area shagreened; galeae shiny or slightly shagreened; maxillary palpal ratio about 2.5:1.8:2.0:1.0; mesoscutum with posteromedian impunctate area reduced to two small areas about four puncture widths in width, surface shiny, with fine reticular shagreening especially peripherally; mesepisterna with punctures large and shallow, surface dulled by fine irregular shagreening; metasomal tergum 1 medially with basal half punctate; tergum 2 with interband zone punctures small, indistinct, separated by one to four puncture widths, surface dulled by fine reticular shagreening, apical area impunctate; tergum 3 like 2 but interband zone punctures more crowded and apical area with sparse minute punctures; pygidial plate V-shaped with rounded apex.

Hair: Head pale ochraceous with brown on vertex. Thorax ochraceous laterally, brown on ventral and anterior surfaces mesepi-

sterna; scutellum brown medially, fringed with ochraceous or ferrugineous; mesoscutum ochraceous to dull ferrugineous with small posteromedial area of brown hairs twice scutellar dark area or smaller; tegulae with or without brown. Metasomal vestiture as in *montana* except as follows: tergum 1 with few or no appressed brown in apical area; tergum 2 with interband zone brown hairs subappressed, those of apical area appressed and minute, distal pale band distinctly interrupted medially, lateral fasciae each equal about two-fifths of width of tergum or more; tergum 3 similar to 2 but basal tomentum brown, distal pale band uninterrupted, and apical area shorter; tergum 4 like 3 but distal band apical and often fringed with brown in median third; tergum 5 and often 6 with lateral ochraceous tufts. Legs as in *montana* but inner surfaces hind basitarsi dark brown to black and scopal hairs brown near apex of basitarsi.

Male. Measurements and ratios: N, 5; length, 9-12 mm.; width, 3-4 mm.; wing length, $M = 3.28 \pm 0.419$ mm.; hooks in hamulus, $M = 11.89 \pm 0.583$; flagellar segment 2/segment 1, $M = 6.81 \pm 0.590$.

Structure and color: Integumental color as in *montana* except as follows: labrum with small mediobasal pale spot sometimes present; clypeus yellow, occasionally narrowly infuscated posteriorly; eyes gray; wing membranes slightly infumate; tergal apices colorless, narrowly hyaline on tergum 1.

Structure as in *montana* except as follows: minimum length first flagellar segment equals one-fifth or less of maximum length second segment; antennae long; maxillary palpal ratio about 14:9:10:1. Sculpture as in female except as follows: mesoscutum with large shallow punctures almost confluent except in small posteromedial area where separated by two or more puncture widths; mesepisternal punctures large, shallow, separated by less than one puncture width, surface dulled by dense shagreening; tergum 1 with basal four-fifths with punctures coarse, dense; tergum 2 with interband zone punctures separated by one to two puncture widths, surface dulled by dense shagreening; terga 3 and 4 similar but with punctures sparser. Sternum 7 and 8 as in *agilis*, median plates of sternum 7 with apical margins converging basomedially, apicoventral tubercle of sternum 8 sharply pointed. Genitalia as in *agilis* (see Michener, 1954, p. 133, figs. 104-106); but sternum 7 with median plates with ventral hairs minute, seemingly glabrous and sternum 8 with ventral tubercle acute.

Hair: Head and thorax ochraceous to dull ferrugineous on dorsum

of thorax except as follows: vertex often with brown; scutellum usually with brown medially; mesoscutum usually with brown posteromedially; tegulae usually without brown. Metasomal vestiture as in *montana* except as follows: terga 2 to 5 with pale distal bands narrow but complete; terga 6 and 7 dark brown. Legs as in *montana*.

Type Material. The holotype female of *persimilis*, collected at Agua Amarillo (= Agua Maria), Honduras, November 17 by Vidales, is in the U. S. National Museum (Type No. 58542), Washington, D. C. The holotype female of *perplexans*, collected at Uyaca Peak, February 9, by W. P. Cockerell, is in the U. S. National Museum (Type No. 58543). The holotype male of *griseihirta* from Uyaca Peak, Honduras, collected by Morales on March 9, is in the U. S. National Museum (Type No. 58544).

Distribution. M. persimilis is known from Guatemala, Honduras and Panamá. In addition to the type material, 3 females and 5 males were examined by the author. Michener (1954) records males from Panamá. These records are listed below.

GUATEMALA: Cunen, August 11, 1947, C. and P. Vaurie; Tecpán, October 9, 1929, D. M. Bates. HONDURAS: Aguas Amarilla, 1 female on November 17; 1 female on December 18. PANAMA: Bambito, Volcan Chiriquí, December, 1946, Krauss; El Volcan Chiriquí, February 25, 26, and 29, 1936, Gertsch and Lutz.

Melissodes (Eumelissodes) manipularis Smith

Melissodes manipularis Smith, 1854, Cat. Hymen. British Museum, part 2, p. 240; Cockerell, 1905, Trans. Amer. Ent. Soc., vol. 31, p. 329; 1907, Ann. Mag. Nat. Hist., ser. 7, vol. 20, p. 127.

M. manipularis is a distinctive bee related to *coreopsis* but not as closely as are other members of the *coreopsis-boltoniae* complex of species. The female of *manipularis* is distinctive in the ochraceous to almost red color of the pale head and thorax hairs, the small size of the mesoscutal dark hair patch, the lack of pale lateral tufts on terga 5 and 6, and the dulled galeae. The male is distinctive in the length of the antennae and of the first and second flagellar segments as described below, and in the shape of the basitibial plates as described below.

Female. Measurements and ratios: N, 7; length, 12-13 mm.; width, about 4.5 mm.; wing length, M = 3.63 ± 0.061 mm.; hooks in hamulus, M = 12.29 ± 0.286; flagellar segment 1/segment 2, M = 1.82 ± 0.032.

Structure and color: Integument black except as follows: apical half of mandible and distitarsi rufescent; flagellum red below, segments 2 to 4 darker basad, segment 2 often wholly brown; eyes gray to green; wing membranes clear, veins reddish brown; first tergum extremely narrowly hyaline at apex; tegulae piceous; tibial spurs yellow.

Structure and sculpturing as in *coreopsis* except as follows: clypeus and supraclypeal area shiny, shagreening sparse and extremely fine if present; galeae dulled above by fine tessellation; second flagellar segment subequal in length to apical width; maxillary palpal ratio about 5.7:4.3:3.7:1.0; posteromedian mesoscutal punctures separated by one to two puncture widths, not markedly impunctate posteromedially, surface unshagreened; mesepisternal punctures smaller than posteromedian mesoscutal punctures, surface shiny; tergum 1 with basal three-fifths with punctures small, separated mostly by one puncture width or less, surface reticulotransversely shagreened, apical area with anterolateral lobes not impunctate but more sparsely so; tergum 2 with interband zone punctures same size as small basal area punctures and separated mostly by two puncture widths or more, surface dulled as in tergum 1, apical area with sparse punctures no wider than twice width of hairs arising from them, surface finely shagreened, shiny; tergum 3 similar to 2 but interband zone punctures more abundant and apical area punctures separated mostly by one to two puncture widths; pygidial plate V-shaped, basal width subequal to length, apex rounded.

Hair: Head ochraceous below to bright ochraceous or reddish near vertex, vertex dark brown. Thorax ochraceous laterally and posteriorly; pale mesoscutal and scutellar hairs bright ochraceous to fox red; mesoscutal dark brown patch equals scutellar in size and not extending forward to a transverse line at anterior margins of tegulae. Tergum 1 with basal area ochraceous, apical area with short, simple, closely appressed, dark brown hairs at least basally and in anterolateral lobes; tergum 2 white basally, distal pubescent band white, narrowly interrupted medially if at all, connected with basal white band at extreme sides, interband zone hairs suberect to subappressed, simple, dark brown, apical area hairs subappressed to appressed, simple, dark brown; tergum 3 similar to 2 but basal tomentum dark brown, distal white band uninterrupted; tergum 4 with apical white pubescent band with dark brown fringe in median third to one-half and often with some brown pubescence medially; terga 5 and 6 without pale lateral tufts; sterna dark brown. Legs

ochraceous except as follows: scopae often yellow; basitibial plates, outer-apical surfaces of tibiae, outer surface fore tarsi dark brown; outer surface middle and hind tarsi brown; inner surface hind basitarsi reddish brown; inner surface hind tibiae red to yellow.

Male. Measurements and ratios: N, 5; length, about 13 mm.; width, about 4 mm.; wing length, M = 3.71 ± 0.314 mm.; hooks in hamulus, M = 12.20 ± 0.374; flagellar segment 2/segment 1, M = 10.07 ± 0.243.

Structure and color: Integument black except as follows: clypeus yellow except brown at tentorial pits and apical margin, occasionally infuscated between tentorial pits; labrum entirely black or with large mediobasal pale spot; mandibles without basal yellow maculae or these extremely small; distitarsi and apical half mandibles rufescent; flagellum yellow to red below (including first segment), dark brown above; eyes gray to green; wing membranes clear to slightly milky, veins dark red to reddish brown; tergal apices infumate, piceous, first tergum usually narrowly translucent yellow, occasionally clear, apically; tegulae piceous; tibial spurs yellow.

Structure and sculpturing as in *coreopsis* with the following exceptions and additions: minimum length first flagellar segment equals one-tenth or less maximum length second segment; maxillary palpal ratio about 6.0:5.3:3.3:1.0; tergum 1 with minute punctures in apical area to within one hair length of apex; tergum 2-4 with apical areas punctate as in female but punctures usually smaller and sparser; basitibial plate short, with relatively straight apical edge and distinct apicoposterior angle. Terminalia as in *agilis*.

Hair: Head ochraceous. Thorax ochraceous laterally, bright ochraceous to dull yellow dorsally with larger scutellar and mesoscutal dark brown patches, mesoscutal dark patch subequal to scutellar. Metasomal tergum 1 ochraceous basally, with short, subappressed, simple, dark brown hairs apically; tergum 2 white basally, distal pubescent band white, often narrowly interrupted medially and connected to basal band at extreme sides, interband and apical areas with abundant suberect to subappressed, dark brown, simple hairs; tergum 3 similar to 2 but basal tomentum brown and distal white band reaches apex at least laterally; tergum 5 without white pubescence or this restricted to short apicolateral fasciae; terga 6 and 7 dark brown; sterna dark brown. Legs ochraceous except inner surfaces tarsi red to yellowish red.

Type Material. Holotype male from Georgia is in the British Museum (Natural History) (Type No. 17-B-1157), London, Eng-

land. The holotype has the labrum with pale mediobasal spot equaling about one-third of surface area and has extremely minute pale basal mandibular spots.

Distribution. *M. manipularis* is known from Florida to North Carolina (Fig. 11). In addition to the holotype, seven females and five males were examined. The data for these is listed below. Cockerell (1907) records this species on *Eupatorium* at Falls Church, Virginia, but this record has not been verified by the author.

Florida: Alachua Co.: 1 male, September 1, 1955, F. L. Wilson; "Fla", Dept. Agriculture, 2 males. Georgia: the holotype male. North Carolina: Southern Pines: 2 females, September 15, 1949, T. B. Mitchell; 2 females, September 15, 1949, on *Chrysopsis* sp., T. B. Mitchell; 1 male, September 10, 1950, T. B. Mitchell; 1 female, September 19, 1953, on *Petalostemum* sp., T. B. Mitchell. Wilmington: 1 female, September 19, 1954, T. B. Mitchell. South Carolina: Aiken: 1 male, September 7, 1951, on *Petalostemum* sp., T. B. Mitchell.

Melissodes (Eumelissodes) comata, n. sp.

This large Mexican species, known only from males from Baja California, is closely related to *M. confusa* and to *M. montana.* It has the sparsely punctate basal area of tergum 2 and the short first flagellar segments as in *confusa.* On the other hand, it has the darker clypeus and vestiture and the more protuberant clypeus of *montana.* The clypeus of *comata* is entirely black or almost so and the surfaces of the clypeus and supraclypeal area are strongly shagreened. The galeae are only lightly shagreened or not at all.

Male. Measurements and ratios: N, 7; length, 11-12 mm.; width 3.5-4.0 mm.; wing length, M = 3.54 ± 0.154 mm.; hooks in hamulus, M = 12.57 ± 0.369; flagellar segment 2/segment 1, M = 8.56 ± 0.124.

Structure and color: Integumental color as in *confusa* except as follows: clypeus entirely black or with a small, subapical, bilobed yellow macula less than one-sixth area of clypeus (in two specimens); eyes dark gray; flagellar segments 3-11 red below, segment 2 dark brown near base shaded to red apically; tergal apices hyaline, colorless apically to yellowish brown basally.

Structure as in *montana* except as follows: minimum length first flagellar segment equals about one-tenth maximum length second segment; maxillary palpal ratio about 2.6:2.0:2.4:1.0. Clypeus with large shallow punctures without distinct anterior margins, separated by half to one puncture width posteromedially and by less

elsewhere, with distinct subapical median carina or boss, surface dulled by coarse reticular shagreening; supraclypeal area impunctate medially, dulled by coarse reticular shagreening; galeae above shiny, shagreening, if present, fine and sparse; lateral areas vertex with minute punctures separated by three to four puncture widths, surface shiny. Mesoscutum with posteromedian area impunctate or with scattered punctures, anteriorly large punctures separated mostly by half to one and one-half puncture widths, surface shiny; scutellum similar to anterior third of mesoscutum; mesepisterna with deep punctures separated mostly by half a puncture width, surface shiny but fine irregular shagreening may be present. Metasomal tergum 1 with basal four-fifths or slightly more with large shallow punctures separated mostly by half to one puncture widths, smaller and sparser near impunctate apical area, surface somewhat dulled by reticulotransverse shagreening; tergum 2 with basal area punctures separated mostly by one to two puncture widths, surface reticularly shagreened, interband zone punctures small, separated mostly by two to three puncture widths or more, surface moderately dulled by reticulotransverse shagreening, apical area impunctate, moderately dull, finely shagreened; terga 3-5 similar to 2 except interband zone more densely and reticularly shagreened and apical areas progressively shorter. Terminalia as in *agilis* but sternum 8 with ventral tubercle acute and sternum 7 with median plates with sparse, minute, ventral hairs.

Hair: Vestiture of long hair. Head white except abundant dark brown on vertex. Thorax white except as follows: scutellum dark brown fringed with white; mesoscutum with posteromedian dark brown patch at least twice as large as scutellar dark area and extending forwards to a transverse line at anterior margins of tegulae; tegulae with dark brown. Metasomal tergum 1 with long white basal hairs, apical area with short, simple, suberect, dark brown hairs; tergum 2 with basal area white, distal pale band white, shorter medially than apical area, interband zone with suberect to erect, brown hairs, apical area with simple, brown, suberect hairs (almost completely worn away in specimens before me); terga 3-5 similar to 2 but basal tomentum dark brown, distal pale bands progressively longer and closer to apex until on tergum 5 it reaches apex across most of tergum (distal band brown medially on tergum 5); terga 6 and 7 brown medially to white laterally; sterna yellow medially to white laterally. Legs white except inner surfaces tarsi yellow.

Type Material. The holotype male and six male paratypes were collected by Ross and Bohart, October 14, 1941, at La Laguna, Sierra

Laguna, Baja California, México. The holotype is in the collection of the California Academy of Sciences, San Francisco. Paratypes are in the collections of the California Academy of Sciences, the Snow Entomological Museum of the University of Kansas, Lawrence, and in the author's collection.

Melissodes (Eumelissodes) expolita, n. sp.

This is a medium-sized bee from the southwest which is similar to *M. coreopsis* but distinctive in both sexes because of the extremely small and scattered punctures on both thorax and abdomen. It does not seem to be closely related to any one group of species, but more closely resembles *coreopsis* than any other species. *M. expolita* also resembles certain species of the *subagilis* group, especially in punctation.

Female. Measurements and ratios: N, 7; length, about 12 mm.; width about 4 mm.; wing length, M = 3.23 ± 0.121 mm.; hooks in hamulus, M = 13.00 ± 0.218; flagellar segment 1/segment 2, M = 1.82 ± 0.043.

Structure and color: Integumental color as in *coreopsis* except eyes gray to greenish blue. Structure and sculpture as in *coreopsis* except as follows: clypeal surface unshagreened; supraclypeal area impunctate or with two or three small punctures, surface shiny; vertex with lateral areas with small round punctures separated by three or four puncture widths or more, surface shiny; maxillary palpal ratio about 2.7:2.3:2.3:1.0; mesoscutal punctures minute, posteromedian area impunctate or with one to four scattered punctures, anteriorly at level of anterior end of parapsidal line punctures separated mostly by two or more puncture widths, surface shiny, unshagreened; scutellar punctures small, medially separated by one to three puncture widths; mesepisternal punctures separated by half to one puncture width, surface shiny; propodeum with dorsal surface irregularly rugose basally, punctate apically, posterior surface sparsely punctate with upper triangular area impunctate, lateral surfaces densely punctate, surfaces shiny, with fine reticular shagreening; metasomal tergum 1 with basal half medially with round shallow punctures separated mostly by one to two puncture widths, surface dulled by coarse reticulotransverse shagreening, apical area and anterolateral lobes impunctate, somewhat dulled by fine reticulotransverse shagreening; tergum 2 with basal area punctures separated mostly by one puncture width, surface reticularly shagreened, interband zone punctures minute, mostly smaller than in basal area,

separated by two to three puncture widths or more, surface as in apical area of tergum 1, apical area impunctate or with minute sparse punctures less than twice diameter of hairs arising from them, surface somewhat shinier than interband zone; tergum 3 similar to 2 but interband zone punctures more abundant and apical area shorter; tergum 4 similar to 3 but apical area absent; pygidial plate somewhat U-shaped with rounded apex and broadening basally.

Hair: Head white to pale ochraceous above. Thorax white laterally, white to pale ochraceous above. Metasomal vestiture as in *coreopsis* except as follows: pubescence generally white; tergum 2 with distal white band as long medially as interband zone and as long as or longer than apical area, uninterrupted; tergum 3 with distal white band reaching apical margin at extreme sides; tergum 4 with white apical band uninterrupted; terga 5 and 6 pale (holotype) to dark brown, white laterally. Legs white except as follows: fore tarsi brown; basitibial plates orange to pale brown; inner surfaces hind basitarsi yellow to yellowish red.

Male. Measurements and ratios: N, 10; length, about 11 mm.; width about 3.5 mm.; wing length, $M = 3.24 \pm 0.192$ mm.; hooks in hamulus, $M = 12.70 \pm 0.423$; flagellar segment 2/segment 1, (9) $M = 6.29 \pm 0.200$.

Structure and color: Integumental color as in *coreopsis* except as follows: first flagellar segment wholly dark brown; wing veins dark brown to black; tegulae piceous; tergal apices hyaline, colorless to slightly smoky, not reddened basally.

Structure as in *coreopsis* except as follows: minimum length first flagellar segment equals more than half its own maximum length and about one-sixth maximum length second segment; maxillary palpal ratio about 2.7:2.7:2.5:1.0. Sculpture as in female except as follows: clypeal punctures shallow, indistinct; mesoscutum with posteromedian area often with scattered minute punctures, anterior sixth often as impunctate as posteromedian area or more so; tergum 1 with basal five-sixths punctate; terga 3-5 similar to 2 but with interband zones more punctate and apical areas progressively shorter to absent in fifth. Terminalia as in *agilis* except as follows: spatha ⅓ as long as broad or slightly longer; gonostyli heavy, with hairs near base short, acute, stout; sternum 7 with lateral plate narrow in apical third, at about one-third from apex equals in width less than one-third length of plate; sternum 8 with ventral tubercle acute.

Hair: Head and thorax white. Metasomal vestiture as in *coreop-*

sis except as follows: generally white; tergum 2 with distal white band uninterrupted medially (unless worn), shorter than or subequal to apical area medially; sterna white. Legs white except inner surfaces hind basitarsi yellow.

Type Material. The holotype female, allotype male, and four female and one male paratypes from 10 miles N. of Tucson, Arizona, were collected on *Encelia farinosa*, April 24, 1955, by G. D. Butler. Seven male paratypes from Arizona are as follows: Tucson: 1 male, May 20, 1935, Bryant; 2 males, April 23, 1953, A. and H. Dietrich. Santa Catalina Mts.: 1 male on *Baileya* sp., April 17, 1955, G. D. Butler; 1 male, May 3, 1937, Bryant. Wickenburg: 2 males, April 30, 1938, J. A. Comstock. In addition, 2 female and 1 male paratypes are as follows: Imperial, California: 1 male, May 1911, J. C. Bridwell. Imuris (12 miles N.), Sonora, México: 1 female on *Chrysothamus* sp., May 11, 1953, R. C. Bechtel and E. I. Schlinger. Santa Ana (8 miles S.), Sonora, México: 1 female, May 11, 1953, R. C. Bechtel and E. I. Schlinger (see Fig. 14 for distribution). The holotype and allotype are the property of the University of Arizona, Tucson, but are deposited on indefinite loan in the Snow Entomological Museum of the University of Kansas, Lawrence. Paratypes are in the collections of the University of Arizona, the Los Angeles County Museum, Los Angeles, California, the California Academy of Sciences, San Francisco, the U. S. National Museum, Washington, D. C., Cornell University, Ithaca, New York, the University of California at Berkeley and in the author's collection.

Melissodes (Eumelissodes) interrupta, n. sp.

This species from Central Mexico is closely related to *persimilis* of Central America. The female of *interrupta* can be distinguished from that of *persimilis* (and from its relatives *montana* and *confusa*) by the broadly interrupted distal pale band of the second tergum and by the pale hairs of the inner surfaces of the hind basitarsi. The male of *interrupta* is less readily identified. It also has the interrupted distal pale band of tergum 2 but this is more narrowly interrupted. The male has extraordinarily long hairs on the head, thorax, and hind legs. In this way it resembles *rufipes* and *comata* (both from Mexico) but differs from the latter in the color of the abdominal vestiture and of the clypeus, respectively.

Female. Measurements and ratios: N, 12; length, 10-14 mm.; width, 3.5-5.0 mm.; wing length, M = 3.58 ± 0.467 mm.; hooks in hamulus, M = 13.00 ± 0.408; flagellar segment 1/segment 2, M = 1.79 ± 0.014.

Structure and color: Integumental color as in *coreopsis* except as follows: flagellar segment 2 black, segments 3 to 10 black below or very slightly reddened (in holotype last three segments slightly reddened); eyes brownish gray; wing veins dark reddish brown; tegulae testaceous.

Structure and sculpture as in *coreopsis* except as follows: clypeal punctures large (larger than mesoscutal punctures), crowded, apicomedian carina short (holotype) or absent, surface shiny, coarse sparse shagreening may be present peripherally; maxillary palpal ratio about 3.4:2.4:2.4:1.0; vertex with lateral area punctures large, separated mostly by one-half to one or slightly more puncture widths, surface shiny; metasomal tergum 1 punctate in basal half to three-fifths, punctures shallow, indistinct, surface reticularly shagreened, apical area impunctate, with anterolateral impunctate lobes; tergum 2 with interband zone punctures minute, separated mostly by two puncture widths or more laterally, by four or five puncture widths medially, apical area impunctate except minute sparse punctures between mesal ends of lateral fasciae; tergum 3 similar to 2 but interband zone punctures more abundant; pygidial plate with rounded apex.

Hair: Head and thorax ochraceous except as follows: vertex with abundant brown, mesepisterna with ventral and anterior surfaces brown, scutellum brown medially, mesoscutum brown posteromedially, and tegulae with brown; mesoscutal dark area about twice size of scutellar; dorsum of thorax with pale hairs yellowish. Metasomal vestiture as in *coreopsis* except as follows: tergum 1 with anterolateral lobes of apical area with sparse, simple brown hairs; tergum 2 with interband zone brown hairs subappressed, apical area brown hairs short and appressed, distal pale band interrupted medially by a gap almost equal to width of lateral fasciae thus resulting fasciae truncate or rounded medially; tergum 3 like 2 but distal pale band uninterrupted, basal tomentum brown, apical area short; terga 6 and 7 with lateral pale tufts (often absent on 7). Legs as in *coreopsis* except inner surfaces hind basitarsi yellow to red.

Male. Measurements and ratios: N, 5; length, 11-14 mm.; width, 3.5-4.5 mm.; wing length, $M = 3.76 \pm 0.322$; hooks in hamulus, $M = 13.00 \pm 0.447$; flagellar segment 2/segment 1, $M = 7.87 \pm 0.128$.

Structure and color: Integumental color as in *coreopsis* except as follows: clypeal apical margin dark brown; labrum without pale spot; first flagellar segment brown, segments 2 to 11 yellow to red

below; terga without rufescent area basad of apical hyaline area.

Structure as in *coreopsis* except as follows: minimum length first flagellar segment about one-eighth maximum length second segment, flagellum in repose surpassing pterostigma; maxillary palpal ratio about 3.0:2.6:2.6:1.0. Sculpturing as in female except as follows: clypeal punctures indistinct; tergum 1 with basal four-fifths or more punctate; tergum 2 with interband zone punctures separated mostly by two to three puncture widths; terga 3 to 5 similar to 2 but interband zone punctures slightly more crowded. Terminalia as in *agilis* but sternum 7 with median plate shorter, shorter than lateral plate.

Hair: Hair long, on vertex of head, anterior third of mesoscutum, mesepisterna, and outer-posterior surface of hind basitarsi many hairs longer than third flagellar segment. Head white to pale ochraceous. Thorax white to pale ochraceous laterally, pale ochraceous above, occasionally with brown on scutellum medially (allotype) and a few brown on mesoscutum; tegulae pale. Metasomal vestiture as in *montana* except as follows: tergum 1 with apical hairs pale ochraceous to white; tergum 2 with interband zone hairs erect, white, apical area hairs long, subappressed, brown, distal pale band usually narrowly interrupted medially; terga 3-4 similar to 2 but distal bands uninterrupted; tergum 5 usually with distal pale band interrupted medially (narrowly in allotype) to absent; terga 6 and 7 brown with pale lateral hairs; sterna yellow medially to white laterally. Legs white or pale ochraceous except inner surfaces tarsi yellow.

Type Material. The holotype female, allotype male, and six female and two male paratypes from Palos Colorados, Durango, México, were collected on August 5, 1947, by C. D. Michener. In addition, three female and two male paratypes from México are as follows: Durango: Palos Colorados: 1 female and 2 males, August 5, 1947, M. A. Cazier; 1 female, August 10, 1947, W. Gertsch. Michoacan: 1 female, July 17, 1953, University of Kansas Mexican Expedition. Two additional females collected by Michener at Palos Colorados, Durango, on August 5, 1947, are assigned to this species, but excluded from the type series because of their excessively small size. The holotype and allotype are in the collection of the American Museum of Natural History, New York City. The paratypes are in the American Museum, the Snow Entomological Museum of the University of Kansas, Lawrence, and in the author's collection.

Melissodes (Eumelissodes) floris Cockerell

Melissodes floris Cockerell, 1896, Ann. Mag. Nat. Hist., ser. 6, vol. 18, p. 290; 1899, Cat. de las Abejas de México, p. 13.

This species from Mexico and Guatemala is known only in the male sex. It resembles closely the males of such species as *confusa* and *montana* from the north, and *persimilis* from Central America. It can be distinguished from *interrupta* by its darker vestiture, from *persimilis* by the longer distal pale band of terga 2 and 3, from *confusa* and *montana* by slight differences in sculpture. It may be nothing more than a local variant of one of the above named species, but nothing should be decided until more specimens are available for study.

Male. Measurements and ratios: N, 1; length, about 10 mm.; width, about 3 mm.; wing length, 2.92 mm.; hooks in hamulus, 12; flagellar segment 2/segment 1, 6.29.

Structure and color: Integumental color as in *coreopsis* except as follows: mandibular bases and labrum black; clypeus with apical margin brown and narrowly infuscated along posterior border (also in holotype); eyes gray; flagellar segments 3 to 10 yellow beneath; wing membranes slightly milky, veins dark brown to black; terga 2 to 5 with apical areas hyaline, not reddened basad of apical areas.

Structure and sculpture as in *coreopsis* except as follows: minimum length first flagellar segment one-fifth (holotype) to one sixth or slightly less maximum length second segment, flagellum in repose reaching pterostigma; maxillary palpal ratio about 12:8:10:5:1; galeae unshagreened above, shiny; supraclypeal area reticularly shagreened; mesoscutal punctures peripherally separated by half to one puncture width, posteromedially by two to three puncture widths, surface shiny or slightly dulled by fine reticular shagreening; metasomal tergum 1 with punctures in basal four-fifths, mediobasally punctures separated by half to two puncture widths and surface dulled by dense coarse reticular shagreening, apically less punctate to impunctate in apical fifth and surface shinier, with reticulotransverse shagreening; tergum 2 with basal area punctures separated mostly by one puncture width, surface reticularly shagreened, interband zone punctures separated mostly by one to two puncture widths, surface dulled by fine reticular shagreening, apical area impunctate; terga 3 to 5 similar to 2; sternum 6 with subapical oblique carinae absent or weak. Termi-

nalia as in *agilis* but sternum 8 with ventral tubercle acute and gonostyli not much capitate.

Hair: Head pale ochraceous with sparse brown on vertex. Thorax pale ochraceous laterally; darker ochraceous to almost ferrugineous above with large posteromedian brown area on mesoscutum and scutellum with large median brown area subequal in size to mesoscutal dark area; tegulae with dark brown. Metasomal vestiture as in *confusa* except as follows: tergum 2 with distal pale band not strongly arched or markedly thinned medially, subequal in length to apical area, interband and apical areas with hairs suberect, dark brown; terga 3-5 similar to 2 but apical areas progressively shorter; terga 6 and 7 brown medially to ochraceous laterally; sterna yellow medially to ochraceous laterally. Legs pale ochraceous except inner surfaces tarsi yellow.

Type Material. The holotype male of *floris* from San Rafael, Veracruz, México, C. H. T. Townsend collector, is in the U. S. National Museum (Type No. 3354), Washington, D. C.

Distribution. M. floris is known only from Mexico and Guatemala. Cockerell (1899) records the species from the lower part of Rio Nautla, México. I have seen one specimen from Guatemala as follows: Secanquin, Alta Ver Paz, December, 1905, G. P. Goll collector (this specimen is in the U. S. National Museum).

Melissodes (Eumelissodes) denticulata Smith

Melissodes denticulata Smith, 1854, Catalogue of the Hymenopterous Insects in the Collection of the British Museum, Part 2, p. 311.

Melissodes senilis Smith, 1854, Catalogue of the Hymenopterous Insects in the Collection of the British Museum, Part 2, p. 311; Provancher, 1888, Additions et Corrections au Volume II de la Faune entomologique du Canada traitant des Hyménoptères, p. 301.

Melissodes perplexa Cresson, 1878, Proc. Acad. Nat. Sci. Philadelphia, vol. 30, p. 206 (new synonymy); Robertson, 1892, Trans. Acad. Sci. St. Louis, vol. 5, p. 582; Bridwell, 1899, Trans. Kansas Acad., Sci., vol. 16, p. 211; Cockerell, 1899, Ent. News, vol. 14, p. 3; Viereck, 1903, Ent. News, vol. 14, p. 119; Cockerell, 1906, Trans. Amer. Ent. Soc., vol. 32, pp. 88, 106, 113; Smith, 1910, Ann. Rep. New Jersey St. Museum for 1909, p. 693; Viereck, 1916, Connecticut Geol. Nat. Hist. Surv., Bull. 22, p. 732; Cresson, 1916, Mem. Amer. Ent. Soc., vol. 1, p. 127; Leonard, 1926, Cornell Univ. Agric. Exp. Sta. Mem. No. 101, p. 1028; Graenicher, 1930, Ann. Ent. Soc. Amer., vol. 23, p. 160; Brimley, 1938, Ins. North Carolina, p. 463.

Melissodes vernoniana Robertson, 1905, Trans. Amer. Ent. Soc. vol. 31, p. 368; 1914, Ent. News, vol. 25, p. 69; 1926, Ecology, vol. 7, p. 379; 1928, Flowers and Insects, p. 8; Pearson, 1933, Ecol. Monogr., vol. 3, p. 381.

M. denticulata and the following species, *M. vernoniae*, are highly distinctive bees and closely related. They seem to be more closely related to *corcopsis* than to any other *Eumelissodes*, but also bear certain resemblance to *rustica* and related species.

The female of *denticulata* and *vernoniae* both have pecularily hooked branches on the scopal hairs as described below. Other species of *Eumelissodes* show this character developed to some degree (see *M. agilis*) but never to the extent shown by these two species. The males of *denticulata* and *vernoniae* have the clypeus white or partly white, rather than the usual yellow and have the metasomal tergal apices infumate to some degree. The males are also distinctive in the short hairs of the legs, particularly of the hind tibiae and basitarsi. Both sexes are sparsely clothed with hair and pubescence. *M. denticulata* is separated from *vernoniae* in the diagnosis of the latter.

Female. Measurements and ratios: N, 20; length, 10-12 mm.; width, 3.0-4.5 mm.; wing length, $M = 3.11 \pm 0.173$ mm.; hooks in hamulus, $M = 11.50 \pm 0.136$; flagellar segment 1/segment 2, $M = 1.98 \pm 0.087$.

Structure and color: Integument black except as follows: apical half of mandibles and distitarsi rufescent; eyes green to bluish green; flagellar segments 3-10 reddish beneath; wing membranes infumate, yellowish brown, veins black; tegulae piceous; tibial spurs yellow.

Clypeus evenly rounded, not protruding forward, oculoclypeal distance equals half minimum diameter first flagellar segment or less, with crowded round punctures separated mostly by half a puncture width or slightly more, surface opaque, densely tessellate; supraclypeal area with abundant punctures, densely tessellate; lateral areas of vertex with punctures separated by one puncture width or less, surface somewhat dulled by irregular shagreening; galeae opaque, densely tessellate, with hairs sparse and short; maxillary palpal ratio about 2.7:2.0:2.0:1.0. Thoracic sculpturing as in *coreopsis* except as follows: posteromedial area of mesoscutum often with small impunctate areas; surface mesoscutum and scutellum usually dulled by fine shagreening or minute tessellation. Metasomal tergum 1 with distinct punctures only in basal half or less, often separated by two to four puncture widths, occasionally a few scattered punctures at about half length of tergum and along sides almost to apex, surface dulled by fine, dense, reticulotransverse shagreening; tergum 2 with basal area punctures round, separated mostly by one to two puncture widths, surface dulled by fine reticular shagreening, interband zone with small, sparse, irregular-sized, shallow punctures, more abundant peripherally, surface dulled by reticulotransverse shagreening, apical

area impunctate or virtually so, surface as interband zone; tergum 3 similar to 2 but basal and interband zones more punctate, apical area with minute scattered shallow punctures in basal half separated mostly by three or more puncture widths; tergum 4 as in 3 but apical area reduced to small, triangular, medial area with minute punctures separated by about 2 puncture widths; pygidial plate V-shaped, longer than basal breadth.

Hair: Head white except abundant dark brown on vertex and on face to level of antennal fossae often mixed brown and white. Thorax white except as follows: scutellum black fringed with white; mesoscutum with large posteromedian brown patch equal twice scutellar dark patch and usually extending forward beyond a transverse line at anterior margins of tegulae; posterior pronotal lobes with at least a few black mixed with the white; tegulae with abundant dark hairs; mesepisterna often with black mixed with the white in upper angles. Metasomal tergum 1 with long sparse white hairs in punctate area, apical area glabrous; tergum 2 white basally, distal pubescence band white, usually interrupted medially so as to form lateral fasciae tapering medially, apical area glabrous or with minute, sparse, simple, closely appressed, brown hairs at least laterobasally, interband zone with appressed, short, simple, sparse, brown hairs; tergum 3 similar but basal tomentum brown, distal band usually not interrupted medially, apical area usually with more abundant short, simple, brown, appressed hairs and interband zone often with scattered white pubescence among the dark appressed hairs; tergum 4 similar to 3 but distal band apical and interrupted medially or almost so by inverted triangle of short, black, subappressed, simple hairs (often worn away); terga 5 and 6 dark brown with white lateral tufts; sterna brown, paler laterally. Legs white except as follows: distitarsi, fore and middle basitarsi, outer surface middle tibiae at least apically, inner surface hind basitarsi, and basitibial plates dark brown; inner surface hind tibiae yellowish red. Scopal hairs ochraceous to white, long, abundant, with branches in apical half almost to apex; branches bend away from rachis and then rather sharply distad to form a pronounced S-shape.

Male. Measurements and ratios: M, 20; length, 8-11 mm.; width, 2.5-3.5 mm.; wing length, M = 2.95 ± 0.198 mm.; hooks in hamulus, M= 10.75 ± 0.216; flagellar segment 2/segment 1, M = 7.06 ± 0.142.

Structure and color: Integument black except as follows: clypeus black with apical margin testaceous and apical half, more or less,

white or cream-colored, pale macula usually trilobed along posterior margin, rarely mostly pale with only posterior margin infuscated, and also rarely mostly black; labrum usually with mediobasal pale spot one-third of area labrum or less in size; apical half of mandibles and distitarsi rufescent; eyes green to bluish green; flagellum yellow to red below except brown first segment; wing membranes slightly infumate, yellowish, veins dark brown; tegulae piceous; tibial spurs yellow; metasomal terga with apical areas piceous, occasionally somewhat reddened.

Minimum length first flagellar segment about one-seventh maximum length second segment, penultimate segment more than three times minimum width, flagellum in repose surpassing pterostigma; maxillary palpal ratio about 3.0:2.5:2.5:1.0. Sculpturing as in female except as follows: clypeal punctures usually larger and shallower; mesoscutum often more abundantly punctate; tergum 1 with basal three-fifths punctate, punctures separated by less than one puncture width mediobasally, sparser and smaller toward apex; tergum 2 with basal area punctures larger, separated by half to one puncture width, interband zone punctures separated mostly by two puncture widths, terga 4 and 5 similar to tergum 3; sterna with reticular shagreening. Terminalia as in *vernoniae*.

Hair: Head white except abundant brown on vertex. Thorax white except scutellum brown fringed with white and large posteromedial mesoscutal brown patch often extending forward to a transverse line at anterior margins of tegulae; tegulae often brown; tergum 1 white basally, apical area with short simple, appressed to subappressed, sparse, brown hairs; tergum 2 as in female but distal pale band often not interrupted and interband and apical area hairs subappressed to suberect and usually longer; terga 3-5 similar to 2 but brown basally; terga 6 and 7 brown; sterna ochraceous to brown medially, paler laterally. Legs white except as follows: distitarsi, fore basitarsi, inner surfaces middle basitarsi brown; inner surface hind basitarsi yellow to red. Hairs of hind basitarsi and tibiae (outer surfaces) short, on tibia no longer than width of tibia, on basitarsus less than twice width of basitarsus.

Bionomics. This species is an oligolege on species of the genus *Vernonia* (Compositae) and seemingly is dependent upon this as a source of pollen. Table X gives a brief summary of the floral data available to the author.

Type Material. The holotype male of *denticulata* from North America is in the collection of the British Museum (Natural History)

(Type No. 17 B 833), London, England. The holotype female of *senilis* from Mount Pleasant, Ohio, is in the British Museum (Natural History) (Type No. 17 A 2618), London, England. Smith (1854, p. 311) at the end of the description of *senilis* states that it comes from the same locality as *denticulata* and is probably the same species, however, he does not state the exact locality for *denticulata* nor is the information on the type itself. Lectotype female of *perplexa* from Georgia is in the collection of the Academy of Natural Sciences of Philadelphia, Pennsylvania (with three female and four male paratypes). Lectotype female, here designated, and lectoallotype male, here designated, of *vernoniana,* from Carlinville, Illinois, collected by Charles A. Robertson, August 7, 1899, on

Table X. Summary of Floral Data for *Melissodes denticulata.*

Plant Data			Records of *M. denticulata*			
Family	Number of genera	Number of species	Number of collections	Number of females	Number of males	Total number of bees
Compositae: *Vernonia* spp.	1	7	84	245	72	317
Other genera	6	6	7	1	13	14
Verbenaceae	1	2	4	0	25	25
Other families (3)	4	4	4	1	3	4
Totals	12	19	99	247	113	360

Verbena stricta, are in the collection of the Illinois Natural History Survey, Urbana, Illinois.

Distribution. M. denticulata ranges from southern Canada west to Ontario and south to Texas and Florida (Fig. 22). It has been collected from May 17 to October 18, but chiefly during August. In addition to the type specimens, 464 females and 272 males have been examined from the localities listed below. Of published records, only those verified by the author are included in this list.

Alabama: Colta; Decatur. Arkansas: Hope; Knob Hill Reservation; Marion Co. Connecticut: Mystic. District of Columbia: Washington; Woodridge. Florida: Yankeetown. Georgia: Lav-

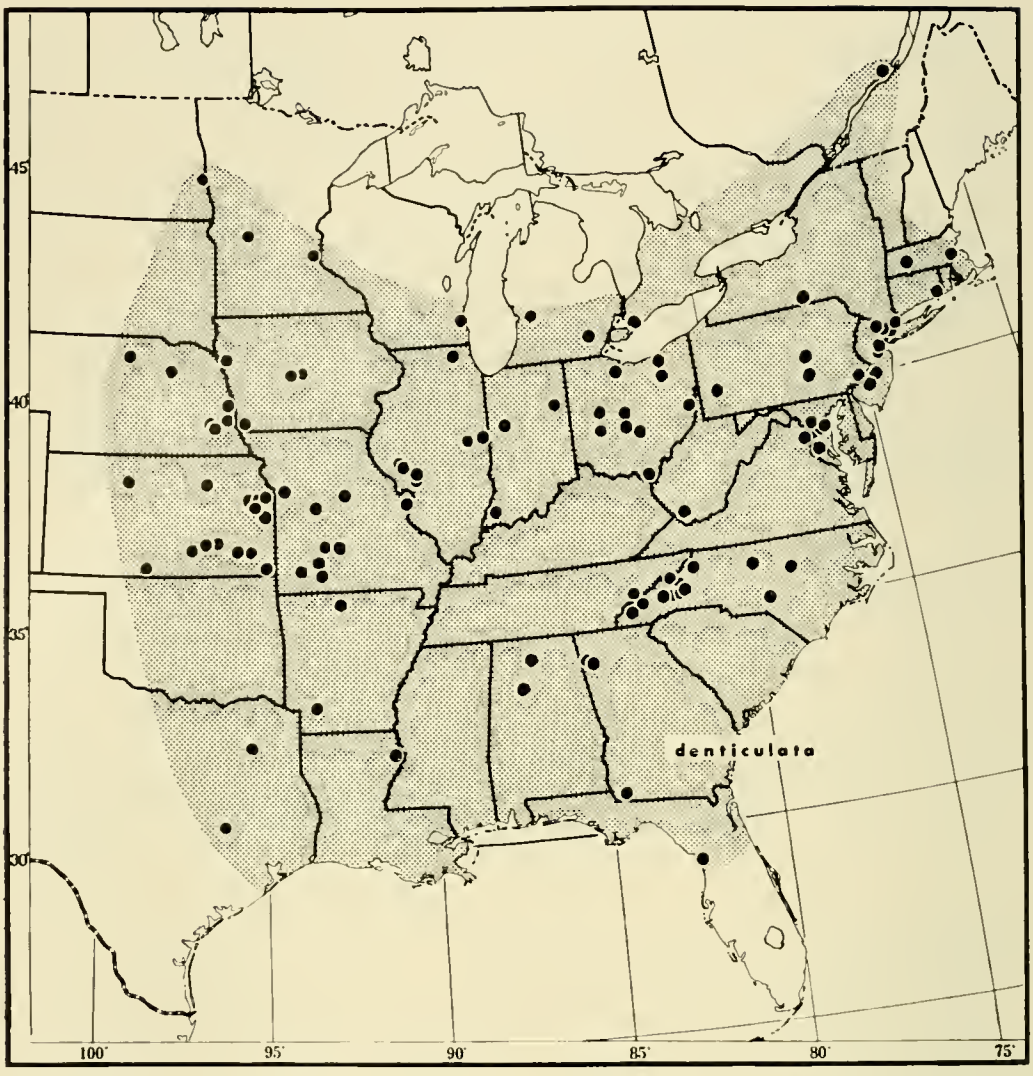


FIG. 22. Map showing the known distribution of *M. (Eumelissodes) denticulata* Smith.

ender, Floyd Co.; Rome; Spring Creek, Decatur Co. ILLINOIS: Algonquin; Bluffs, Scott Co.; Carlinville; Champaign Co.; Danville, Macoupin Co.; Scott Co. INDIANA: Bluffton; Fort Branch. IOWA: Ames; Fremont Co.; Ledges State Park; Sioux City. KANSAS: Baldwin; Barber Co.; Cherokee Co.; DeSoto, Johnson Co.; Douglas Co.; El Dorado; Lawrence; Neosho Co.; Osawatomie; Reece; Riley Co.; Rooks Co.; Sunflower (10 miles E. of Lawrence); Wichita (Air Force Base); Wilson Co. LOUISIANA: Tallulah. MARYLAND: Cabin John; Glen Echo; Indian Head; Patuxent. MASSACHUSETTS: Chicopee; Forest Hills. MICHIGAN: Ann Arbor; Grand Rapids. MINNESOTA: Grey Eagle; St. Anthony Park, Ramsey Co. MISSOURI: Atherton; Buffalo; Columbia; Lebanon; Ozark; St. Louis; Sedalia; Springfield; Verona. NEBRASKA: Lincoln; Louisville; Malcolm; Neligh; Omaha; Rock Co. NEW JERSEY: Alpine, Bergen Co.; Clementon; Jamesburg;

New Brunswick; Pemberton; Ramsey; Riverton. New York: Bronx; New Rochelle; Sheephead; Staten Island; Tioga Co. North Carolina: Asheville; Barber; Black Mts. (Valley of); Bryson City; Busick; Greensboro; Marion; Mt. Mitchell Game Refuge; Nontahala Gorge; Raleigh; Southern Pines; Swannanoa; Watauga Co.; Yancy Co. North Dakota: Fargo. Ohio: Barberton; Cleveland; Delaware Co.; Franklin Co.; Fremont; Ironton; Logan Co.; Mount Pleasant; Pickerington; Springfield. Pennsylvania: Highspire; North Braddock; Northcumberland; Philadelphia. Tennessee: Great Smoky Mountain National Park; Hattiesburg. Texas: Brazos Co.; Mineola. Virginia: Barcroft; Falls Church; Glencarlyn; Goshen; Rosslyn (along Potomac River). West Virginia: Baileysville. Wisconsin: Milwaukee. *Canada.* Ontario: Chatham. Quebec: Cap Rouge. In addition to the above, two males doubtfully labeled have been examined; one from Monticello, Utah, collected by G. F. Knowlton and G. E. Bohart, July 15, 1952, and the second from Pullman, Washington, collected by C. V. Piper. The author is quite certain that the Washington specimen was mislabeled; however, the Utah specimen could well be a stray male carried out of range by man or blown there by storms.

Flower Records. Amphiachyris dracunculoides, Carduus crispus, Convolvulus sepium, Eupatorium purpurea, Ipomoea pandurata, Pycnanthemum sp., *Silphium* sp., *S. laciniatum, Solidago juncea, Symphoricarpos* sp., *Verbena* sp., *V. hastata, V. stricta, Vernonia* sp., *V. altissima, V. baldwini, V. b. interior, V. fasciculata, V. glauca, V. noveboracensis, V. texana.*

Melissodes (Eumelissodes) vernoniae Robertson

Melissodes vernoniae Robertson, 1902, Canadian Ent., vol. 34, p. 323; 1905, Trans. Amer. Ent. Soc., vol. 31, p. 368; Cockerell, 1909, Ann. Mag. Nat. Hist., ser. 8, vol. 4, p. 26; Graenicher, 1911, Bull. Pub. Museum Milwaukee, vol. 1, p. 247; Robertson, 1914, Ent. News, vol. 25, p. 69; 1926, Ecology, vol. 7, p. 379; 1928, Flowers and Insects, p. 8; Pearson, 1933, Ecol. Monogr., vol. 3, p. 378; Graenicher, 1935, Ann. Ent. Soc. Amer., vol. 28, p. 304.
Melissodes confusiformis incondita Cockerell, 1925, Ann. Mag. Nat. Hist., ser. 9, vol. 16 (new synonymy); 1928, Univ. Colorado Studies, vol. 16, p. 114.

M. vernoniae is closely related to *denticulata* but averages somewhat larger in size and paler in color. The female of *vernoniae* can be told from that of *denticulata* by the usual lack of dark hairs mixed with the pale on the posterior pronotal lobes and the mesepisterna (although not in all specimens), and the clear, colorless or slightly milky wing membranes. The male of *vernoniae* is readily distinguished from that of *denticulata* by the shorter an-

tennae and slightly longer first flagellar segments, the clypeus usually being entirely pale, and by the mandibles usually having pale basal maculae.

Female. Measurements and ratios: N, 20; length, 11-15 mm.; width, 4.0-5.5 mm.; wing length, M = 3.85 ± 0.152 mm.; hooks in hamulus, M = 13.95 ± 0.276; flagellar segment 1/segment 2, M = 1.90 ± 0.022.

Structure and color: Integumental color as in *denticulata* except as follows: often entire legs except coxae rufescent; eyes gray to bluish gray; wing membranes clear, colorless or slightly milky, veins usually reddish brown; tergum 1 with extremely narrow hyaline apical margin.

Structure and sculpturing as in *denticulata* except as follows: supraclypeal area often moderately shiny; lateral areas of vertex with punctures separated by one to two puncture widths, shiny, shagreening slight; maxillary palpal ratio about 3.0:2.7:2.0;1.0; tergum 1 with punctures of basal half mostly separated by one puncture width or less; tergum 2 with basal area punctures separated mostly by less than one puncture width; tergum 4 with apicomedial, inverted triangular area lacking.

Hair: Head white except abundant brown on vertex. Thorax white except scutellum brown fringed with white, mesoscutum with large posteromedian brown patch which usually extends forward at least to a transverse line at anterior margins of tegulae (occasionally smaller), and pale anterior mesoscutal hairs usually ochraceous; occasionally with brown mixed with white on posterior pronotal lobes; tegulae usually with brown. Metasomal hairs as in *denticulata* except as follows: tergum 2 with distal band broader and occasionally not interrupted medially or only narrowly so, interband zone and apical area hairs when present pale, brown; terga 3 and 4 with broader distal pale bands and tergum 4 with inverted triangular, apicomedial area of simple brown hairs lacking. Legs as in *denticulata* but with less brown; tibiae often without brown on outer surfaces; inner surface hind basitarsi often reddish brown; scopal hairs as in *denticulata.*

Male. Measurements and ratios: N, 20; length, 10-14 mm.; width, 3.0-4.5 mm.; wing length, M = 3.78 ± 0.215 mm.; hooks in hamulus, M = 13.15 ± 0.166; flagellar segment 2/segment 1, M = 5.80 ± 0.101.

Structure and color: Integumental color as in *denticulata* except as follows: clypeus usually entirely white or cream-colored except

testaceous apical margin and dark tentorial pits, occasionally infuscated along posterior margin between tentorial pits (especially in specimens from Missouri); labrum with pale mediobasal spot; mandibles usually with basal white maculae; distitarsi and often basitarsi and tibiae rufescent; terga with apical margins usually broadly hyaline, colorless or yellow, occasionally infumate and rarely piceous; wing membranes clear, colorless, veins reddish brown to brown.

Minimum length first flagellar segment about one-sixth maximum length second segment or more, penultimate segment slightly more than three times as long as broad, flagellum in repose usually not quite reaching pterostigma and never surpassing. Maxillary palpal ratio about 8:5:4:1. Sculpturing as in female except as follows: basal half of galeae occasionally shiny and unshagreened; posteromedial mesoscutal impunctate area reduced and often absent; tergum 1 punctate in basal three-fifths, punctures separated mostly by two or more puncture widths. Terminalia as in *agilis* (Figs. 92-95).

Hair: Head white but often with brown on vertex. Thorax white to ochraceous (above) with abundant brown on scutellum and posteromedial mesoscutal brown patch equals twice scutellar dark patch or less, occasionally with no or very few brown hairs on mesoscutum; tegulae usually with brown. Metasomal hairs as in *denticulata* but tergum 2 with distal pale band usually not interrupted medially, terga 3 and 4 with distal pale bands usually broader, and tergum 5 usually with a complete distal pale band. Legs as in *denticulata*.

Bionomics. *M. vernoniae*, as the name implies, is an oligolege of the genus *Vernonia* (Compositae) and, like its relative *M. denticulata*, is seemingly dependent upon that genus as a source of pollen. However, *vernoniae* has been collected more often on other plants than has *denticulata* and it seems probable that it may use pollen from *Helianthus* spp. and possibly *Ipomoea* spp. on occasion. Table XI summarizes the available floral data.

Type Material. Lectotype female, here designated, August 19, 1902, and lectoallotype male, here designated, August 16, 1902, both collected by Charles A. Robertson on *Vernonia fasciculata* at Carlinville, Illinois, are in the collection of the Illinois Natural History Survey, Urbana. Sixteen female and sixteen male paratypes from the same flower and locality are with the lectotypes. Holotype female of *confusiformis incondita* from Wray, Colorado, collected by

TABLE XI. Summary of Floral Data for *Melissodes vernoniae*.

Plant Data			Records of *M. vernoniae*			
FAMILY	Number of genera	Number of species	Number of collections	Number of females	Number of males	Total number of bees
Compositae: *Vernonia* spp.	1	5	59	345	142	487
Other genera	8	10	16	13	5	18
Other families (5)	6	6	9	22	8	30
Totals	15	21	84	380	155	535

F. E. Lutz on August 17-19, 1919, is in the collection of the American Museum of Natural History, New York City.

Distribution. The species ranges from Indiana and North Dakota west to southern Idaho and south to New Mexico and Texas (Fig. 23). It has been collected from May 30 to September, but chiefly in July and August. In addition to the types, 480 females and 253 males have been examined from the localities listed below. This list includes only those published records verified by the author.

ARKANSAS: Lawrence Co.; Marion Co. COLORADO: Denver; Fort Collins; Wray. IDAHO: Franklin. ILLINOIS: Carlinville; Champaign; Danville; Macoupin Co.; Monticello; Peoria; White Hall. INDIANA: Fort Branch. IOWA: Ames; Ledges State Park. KANSAS: Allen Co.; Anderson Co.; Baldwin; Butler Co.; Clay Center; Delavan (5 miles E.); Harvey Co.; Iola; Kingman Co.; Labette Co.; Lake View, Douglas Co.; Lawrence; Linn, Washington Co.; Manhattan; Neosho Co.; Olathe; Onaga; Osawatomie; Osborne Co.; Ottawa; Riley Co.; Scott Co.; Sunflower (10 miles E. of Lawrence); Topeka; Washington Co.; Wellington; Wichita (Air Force Base); Wilson Co. MISSOURI: Buffalo; Columbia; Lebanon; Ozark; St. Louis; Smithton, Pettis Co.; Strasburg (5 miles W.); Verona. NEBRASKA: Aurora; Carns; Fairmont; Glen, Sioux Co.; Hardy; Lincoln; Louisville; Malcolm; McCool; Omaha. NEW MEXICO: Quemado; Roswell. NORTH DAKOTA: Fargo. SOUTH DAKOTA: Custer. TEXAS: Alpine; Blanco Co.; Brazos Co.; Clarendon; Comfort; Conlen; Dallas; Davis Mts. (Limpia Canyon); Dawn; Fedor, Lee Co.; Fort Davis, Jeff Davis Co.; Hereford (5 miles S. W.); Llano; Waco.

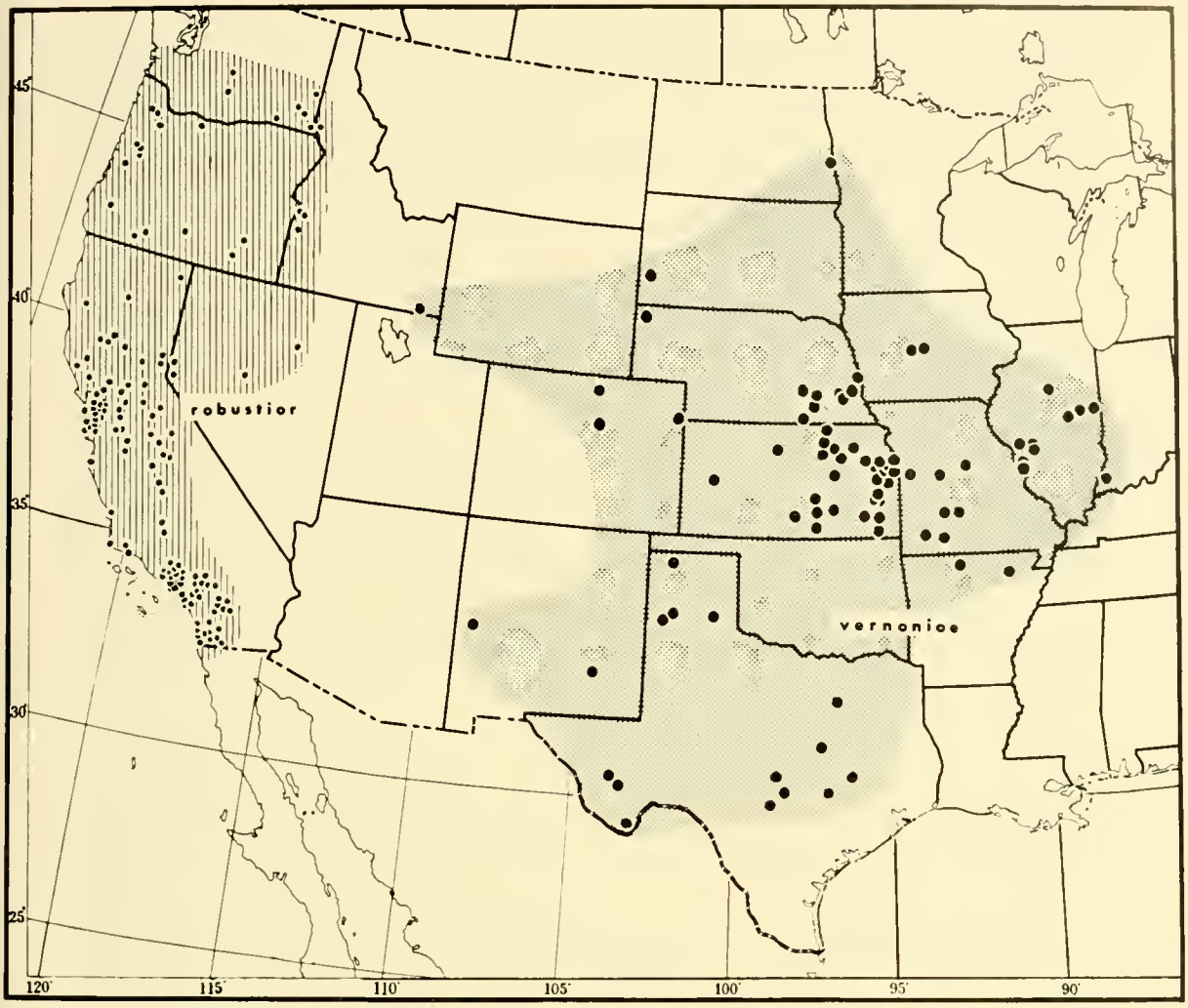


FIG. 23. Map showing the known distributions of *M. (Eumelissodes) vernoniae* Robertson and *M. (E.) robustior* Cockerell.

Flower Records. Bidens sp., *Gaillardia pulchella, Grindelia* sp., *Helianthus* sp., *H. tuberosus, Heliopsis helianthoides, Ipomoea pandurata, Lacinaria* sp., *Lactuca pulchella, Liatris* sp., *Monarda fistulosa, Polygonum* sp., *Rudbeckia* sp., *R. hirta, Silphium laciniatum, S. speciosum, Verbena* sp., *V. stricta, Vernonia* sp., *V. altissima, V. fasciculata, V. interior baldwini, V. longifolia, V. texana.*

Melissodes (Eumelissodes) robustior Cockerell

Melissodes robustior Cockerell, 1915, Ann. Mag. Nat. Hist., ser. 8, vol. 16, p. 482; 1930, Ann. Mag. Nat. Hist., ser. 10, vol. 5, p. 405.

This is one of the most abundant species of *Eumelissodes* found along the Pacific Coast. It is a medium-sized to large bee related to *M. coreopsis*, although not closely. The female is like that of *coreopsis* in color and sculpture but have the galeae dulled by dense

tessellation, the pale vestiture ochraceous to dull rufescent, abundant dark hairs on the tegulae, and wings with reddish brown veins and slightly infumate (yellowish) membranes. The male of *robustior* is readily distinguished from that of *coreopsis* by the longer first flagellar segments, the tessellate galeae, and the yellowish wing membranes.

Female. Measurements and ratios: N, 20; length 10-15 mm.; width, 3.5-5.5 mm.; wing length, M = 4.13 ± 0.261 mm.; hooks in hamulus, M = 14.70 ± 0.262; flagellar segment 1/segment 2, M = 2.03 ± 0.027.

Structure and color: Integument black except as follows: apical half of mandibles and distitarsi rufescent; flagellar segments 3-10 red to reddish brown below; eyes dark gray to slightly greenish gray; tegulae piceous to somewhat rufescent; wing membranes hyaline, slightly infumate, yellowed, veins dark reddish brown; tibial spurs yellow to rufescent; tergum 1 rufescent to translucent-yellow apically.

Structure and sculpture as in *coreopsis* except as follows: clypeal punctures irregularly round, crowded, separated mostly by half a puncture width or less, surface dulled by coarse shagreening; supraclypeal area usually dulled by fine reticular shagreening, with few or no punctures medially; lateral areas of vertex with punctures minute, separated by three or four puncture widths or more, surface shiny; galeae opaque above, dulled by dense tessellation and distinct punctures; maxillary palpal ratio about 9:8:7:1, fourth segment occasionally slightly longer, occasionally virtually absent. Mesoscutal punctures small, round, posteromedially separated mostly by half to two puncture widths, surface unshagreened; scutellum similar; mesepisternal punctures larger, extremely shallow, often with bottoms slightly dulled and surface dulled by fine irregular shagreening. Metasomal sculpturing as in *coreopsis* except as follows: tergum 1 with basal three-fifths with punctures separated mostly by one to two puncture widths; tergum 2 with basal area punctures small, separated mostly by one to two puncture widths, surface with fine reticular shagreening, interband zone punctures small, separated mostly by two to three puncture widths, surface reticularly shagreened, apical area impunctate; terga 3 and 4 similar but interband zone punctures more crowded. Pygidial plate V-shaped, longer than broad.

Hair: Head white to pale ochraceous with brown on vertex and ochraceous on occipital area. Thorax pale ochraceous to white

laterally and posteriorly, ochraceous above with scutellum dark brown and ochraceous peripherally and mesoscutum with postero-median dark brown patch usually twice as large as scutellar, but often less; tegulae with dark brown. Tergum 1 ochraceous to pale ochraceous basally, glabrous apically; tergum 2 with basal area white, distal pale band white to pale ochraceous, broad, usually not interrupted medially although narrowed or notched posteriorly, interband zone with abundant, short, erect, dark brown hairs, apical area with short, suberect to appressed, dark brown hairs, tergum 3 similar to 2 but basal tomentum brown, distal pale band broader and often reaching apical margin at extreme sides; tergum 4 with pale band distal, not interrupted medially or fringed with dark; terga 5 and 6 with pale lateral tufts; sterna yellow to pale brown medially, white laterally. Legs pale ochraceous except as follows: outer surfaces fore and middle tarsi, outer-apical surfaces fore and middle tibiae, and basitibial plates brown; inner surfaces fore and middle tarsi reddish brown; inner surfaces hind basitarsi dark red to reddish brown; inner surfaces hind tibiae yellow.

Male. Measurements and ratios: N, 20; length, 10-14 mm.; width, 3-4 mm.; wing length, $M = 3.80 \pm 0.149$ mm.; hooks in hamulus, $M = 13.60 \pm 0.239$; flagellar segment 2/segment 1, $M = 3.87 \pm 0.064$.

Structure and color: Integument black except as follows: clypeus yellow except testaceous apical border and dark tentorial pits; labrum with mediobasal spot; mandibles without basal yellow spots; flagellar segments 2-11 yellow to red beneath, segment 1 occasionally red; apical half of mandibles and tarsi rufescent; eyes brown to yellowish green or gray; wing membranes clear, slightly infumate, yellowish especially in vicinity of veins, veins dark red to reddish brown; tegulae piceous; tibial spurs yellow to red; tergal apices hyaline, colorless to yellow.

Clypeus as in *coreopsis;* supraclypeal area and galeae as in female; minimum length first flagellar segment usually equals one-fourth to one-fifth maximum length second segment; maxillary palpal ratio about 9:8:6:1, fourth segment often virtually absent. Mesosomal and metasomal sculpture as in female except as follows: tergum 1 with basal four-fifths punctate; tergum 2 with interband zone punctures slightly larger and separated mostly by two to three puncture widths; terga 4 and 5 like tergum 2. Terminalia as in *agilis* but sternum 8 with ventral tubercle lamellate, not strongly pointed near apex.

Hair: Clypeus and genal areas white to pale ochraceous, vertex ochraceous, often with brown. Thorax ochraceous above, paler laterally and posteriorly; scutellum with abundant brown hairs medially; mesoscutum with posteromedial brown patch at least equal in area to scutellar dark patch and often twice as large; tegulae with brown hairs. Tergum 1 with long pale ochraceous hairs basally, reaching margin across entire tergum, appressed apically; tergum 2 white to pale ochraceous basally, distal pale pubescent band narrow and often interrupted medially, interband zone hairs long, erect to suberect, pale ochraceous, apical area hairs usually abundant (often worn away), suberect to appressed, pale ochraceous; terga 3-5 similar to 2 but distal pale bands not interrupted and progressively closer to apical margin, often apical on tergum 5; terga 6 and 7 ochraceous to golden; sterna yellow medially to almost white or pale ochraceous laterally. Legs pale ochraceous to white except inner surfaces tarsi yellow.

Bionomics. *M. robustior* is a composite oligolege and seems to prefer the genus *Helianthus* to all others. Considerable flower data are available and these are summarized in the table XII below.

Type Material. Holotype female of *robustior* from Berkeley, California, collected by T. D. A. Cockerell, August 9, 1915, on *Helian-*

TABLE XII. Flower Data for *Melissodes robustior.*

Plant Data			Records of *M. robustior*			
FAMILY	Number of genera	Number of species	Number of collections	Number of females	Number of males	Total number of bees
Compositae: *Helianthus* spp.	1	5	63	60	118	178
Coreopsis spp.	1	3	40	19	56	75
Cosmos sp.	1	1	11	24	8	32
Heterotheca sp.	1	1	10	5	6	11
Other genera	18	24	66	40	86	126
Other families (6)	6	7	7	0	8	8
Totals	28	41	197	148	282	430

thus annuus, is in the collection of the U. S. National Museum, Washington, D. C.

Distribution. M. robustior ranges throughout the Pacific Coast States east to Idaho and Nevada (Fig. 23). It has been collected from May 2 to October 29, but chiefly in June, July and August. In addition to the holotype, 296 females and 659 males were examined from the localities listed below.

CALIFORNIA: Alameda; Alameda Foothills, Altadena; Alum Rock Park, Santa Clara Co.; Anaheim; Antioch; Anza (2 miles E.); Artesia; Artois; Arvin; Auburn; Avon; Bakersfield; Banning; Bayliss; Berkeley; Big Dalton Dam, Los Angeles Co.; Brisbane; Calistoga; Calpine; Carmel; Clear Lake; Cloverdale; Clovis; Contra Costa Co.; Corona; Coronado; Davis; Dinckey Ranger Station, Fresno Co.; Dos Palos; Eagle Rock Hills, Los Angeles Co.; Echo Lake, Shasta Co.; El Toro; Encinitas; Gavilon; Glendale; Glenn Co.; Hagerman Park, Merced Co.; Hallelujah Junction; Hamilton City; Hayward; Hemet; Hillsboro; Huntington Park; Idlewild; Indio; Irvington; Jacumba; Laguna Beach; Laguna Mt., San Diego Co.; Lake City; Lake Tahoe; Lindsay; Lodi; Lompoc; Los Angeles; Los Angeles Co.; Mariposa Co.; Marsh Creek Canyon, Contra Costa Co.; Martinez; Midway City; Mill Creek; San Bernardino Co.; Mira Loma; Mokelumna Hill; Morro Bay; Mountain View; Mount Diablo; Newport Beach; Nippinnawassee, Madera Co.; Oak Grove; San Diego Co.; Oakland; Oakley; Oceanside; Ontario (6 mi. E.); Oroville; Pasadena; Patterson; Pine Crest; Pine Valley; Poway; Rawhide; Redlands; Redwood City; Rialto; Riverside; Rivera; Sacramento; Sacramento Co.; San Bernardino Co.; San Bernardino Mts.; San Diego; San Diego Co.; San Francisco; San Gabriel Mts.; San Jose; Santa Barbara; Santa Barbara Foothills; Santa Cruz Mts.; Santa Monica; Shaver Lake, Fresno Co.; Sierraville; Sierra Madre (near Los Angeles); Snowline Camp, Eldorado Co.; Stanford University, Stockton; Tanbark Flat, Los Angeles Co.; Turlock; Twain Harts, Tuolumne Co.; Upper Santa Ana River, San Bernardino Co.; Vacaville, Vallejo; Vandervanter Flat, San Jacinto Mts.; Vernalis; Visalia; Warrens; West Hollywood Hills; Westwood Hills, Los Angeles Co.; Whittier; Wrightwood; Yosemite National Park (Crane Flat); Yucaipa. IDAHO: Lewiston; Parma; Regina (12 miles N. W.); Squaw Creek (10 miles E. of Emmet), Gem Co. NEVADA: Austin; Elko; Reno. OREGON: Aurora; Bane Island, Klamath Lake; Blooming; Catlow Valley, Harney Co.; Cornelius; Corvallis; Fish Lake; Lane Co.; Riddle; Salem; Shedd; Summer Lake; Ten Cent Lake (dry),

East of Steens Mts.; The Dalles (14 miles E.). WASHINGTON: Asotin (Snake River); Lone Tree, Yakima River; North Yakima; Penawawa; Walla Walla; Wawawai.

Flower Records. *Asclepias* sp., *Aster* sp., *Brassica adpressa, B. incana, Centromadia pungens, Chaenactis artemesiaefoliae, C. glabiuscula, Chrysothamnus* sp., *Cichorium* sp., *Cirsium* sp., *C. lanceolatum, Coreopsis* sp., *C. grandifolia, C. lanceolata, C. tinctoria, Corethrogyne* sp., *C. bernardense, Cosmos* sp., *Encelia* sp., *E. californica, E. farinosa, Ericameria palmeri, Gaillardia* sp., *Goddetia bottae, Grindelia* sp., *G. camporum, G. eleta, Gutierrezia californica, G. sarothrae, Helianthus* sp., *H. annuus, H. bolanderi, H. gracilenthus, H. lenticularis, H. petiolaris, Hemizonia* sp., *H. paniculata, H. wrightii, Heterotheca grandiflora, Isocoma vernonioides, Lactuca* sp., *Lythrum californicum, Marrubium vulgare, Scabiosa atropurpurea, Senecio* sp., *S. douglasii, Solidago* sp., *S. californica, Stephanomeria* sp., *S. exigua.*

Melissodes (Eumelissodes) hurdi, n. sp.

This medium-sized bee from California is a close relative of *M. robustior.* It has been named in honor of Dr. P. D. Hurd of the University of California who collected the holotype and many of the paratypes and who has collected many species of *Melissodes* in California, Arizona and Mexico. The females of *hurdi* can be separated from those of *robustior* by the lack of brown mesoscutal, tegular and scutellar hairs (although there occasionally are a few dark scutellar hairs), by the fine but conspicuous punctures of the apical areas of terga 2 and 3, and by the colorless wings. The males of *hurdi* are distinctive in the partially black clypeus, the strongly crenulate flagellum, the dulled galeae, and the suberect dark hairs of the apical areas of terga 2 to 4.

Female. Measurements and ratios: N, 20; length 10-13 mm.; width, 4-5 mm.; wing length, $M = 3.59 \pm 0.224$ mm.; hooks in hamulus, $M = 15.35 \pm 0.233$; flagellar segment 1/segment 2, $M = 2.11 \pm 0.028$.

Structure and color: Integumental color as in *robustior* except as follows: wing membranes colorless to milky, veins dark brown to black. Structure and sculpture as in *robustior* except as follows: clypeal surface only slightly dulled by fine reticular shagreening; supraclypeal area with a few large punctures medially, shiny, with fine irregular shagreening; galeae tessellate above; maxillary palpal ratio about 3.8:3.4:2.4:1.0; second flagellar segment as long below

as maximum width or shorter; metasomal tergum 1 with basal four-fifths or slightly less with round punctures separated mostly by half to one puncture width, apical area impunctate with small antero-lateral impunctate or sparsely punctate lobes; tergum 2 with basal area punctures separated by one puncture width or slightly more, interband zone punctures small, separated by one to two puncture widths, apical area with minute but distinct punctures separated mostly by three puncture widths, surface shiny; tergum 3 similar to 2 but interband zone punctures denser and apical area punctures separated mostly by one to two puncture widths; pygidial plate V-shaped, apex rounded, longer than broad.

Hair: Head white to pale ochraceous with sparse brown hairs on vertex. Thorax white to pale ochraceous laterally, ochraceous dorsally, occasionally a few brown hairs medially on scutellum. Metasomal vestiture as in *robustior* except as follows: tergum 1 with long, appressed, ochraceous to white, barbed hairs reaching from apical margin of punctate area to apical margin of tergum forming pale apical band (unless worn), pale ochraceous basally; tergum 2 with interband zone hairs suberect to erect, pale ochraceous to white, distal pale band white to pale ochraceous, not reaching apex of tergum except occasionally at extreme sides, longer medially than apical area, apical area with abundant, suberect, simple, dark brown hairs; tergum 3 similar to 2 but interband zone erect hairs at least partly brown and apical area shorter and usually lacking laterally; tergum 4 like 3 but lacking apical area; terga 5 and 6 dark brown with pale lateral tufts. Legs as in *robustior* except as follows: outer surfaces middle basitarsi pale ochraceous; inner surfaces hind basitarsi red to reddish brown.

Male. Measurements and ratios: N, 20; length, 9-13 mm.; width, 2.5-4.0 mm.; wing length, $M = 3.44 \pm 0.135$ mm.; hooks in hamulus, $M = 12.94 \pm 0.211$; flagellar segment 2/segment 1, $M = 5.88 \pm 0.111$.

Structure and color: Integumental color as in *robustior* except as follows: clypeus light yellow with brown apical border and infuscated posterior margin to posterior two-thirds black; labrum black; flagellar segment 1 and base of 2 brown; eyes yellowish green (holotype) to gray; wing membranes colorless or milky, veins dark red to brown.

Structure as in *robustior* except as follows: minimum length first flagellar segment one-fourth to one-fifth maximum length second segment, penultimate segment more than three times as long

as broad, segments 3 or 4 to 10 strongly crenulated by basal constrictions; maxillary palpal ratio about 4.0:3.8:3.0:1.0; sternum 6 with distinct subapical carinae but these less than half as long as distance between their distal tips and sternum with distinct median shiny sulcus. Sculpture as in female except as follows: clypeal punctures less distinct; tergum 1 punctate almost to apical margin but punctures smaller in last fifth; terga 2-4 with interband zone punctures coarser and apical area punctures less distinct. Terminalia as in *agilis* but sternum 8 with ventral tubercle lamellate and strongly pointed apically, higher than in *robustior.*

Hair: Head and thorax white to pale ochraceous, occasionally with brown on scutellum (holotype). Metasomal vestiture as in *robustior* except as follows: tergum 1 often (holotype) with some apicomedian hairs brown; tergum 2 with distal pale band subequal in length to apical area medially, uninterrupted, apical area with abundant, suberect, dark brown hairs; terga 3 and 4 simliar to 2 but apical areas progressively shorter and on tergum 4 distal pale band reaches margin of tergum laterally; tergum 5 similar but lacking apical area; terga 6 and 7 brown to ochraceous. Legs as in *robustior.*

Notes. In spite of the resemblance of *M. hurdi* to *M. robustior, hurdi* is perhaps more closely related to the *menuachus* group as is indicated by the crenulate male antennae, the pale distal band on tergum 1 of the female and the lack of brown mesoscutal hairs on both sexes. The *menuachus* group seems to relate to the *coreopsis* group through the *robustior* group of species, therefore including *hurdi* in the same group with *robustior* does no violence to the phylogeny of the genus.

Type Material. The holotype male, allotype female, and four female paratypes were collected at Antioch, California, August 9, 1947, by P. D. Hurd. In addition, 41 female and 29 male paratypes from Antioch, California, are as follows (given by year collected); 1934: 1 female, September 14, B. J. Hall; 2 females and 3 males, September 9, G. E. and R. M. Bohart. 1935: 1 male, September 15, G. E. and R. M. Bohart. 1936: 2 females, August 23, 2 females and 1 male, August 30, 2 females, September 9, 2 females, September 13, 2 females, October 17, E. C. Van Dyke; 1 female on *Erigonum* sp., 1 female on *Grindelia* sp., 1 female in sand dunes, and 1 male on *Gutierrezia californica,* September 12, E. G. Linsley; 1 female, September 5, 1 female, September 10, M. A. Cazier; 1 female, August 8, 1 female and 1 male, August 9, C. D. Michener; 1 male, August 10, 1 female, October 10, G. E. Bohart; 1 male, September

10, G. E. and R. M. Bohart; 2 males, September 20, G. Ferguson. 1937: 1 male, September 26, K. S. Snyder; 1 female, July 15, 1 female, October 10, E. C. Van Dyke. 1938: 1 female, September 9, T. Aitken; 1 female, September 9, E. C. Van Dyke. 1939: 1 male, September 16, B. Brookman. 1947: 1 female and 1 male, October 13, 2 males, September 10, P. D. Hurd. 1948: 1 male, September 8, J. W. MacSwain; 2 males, September 8, 1 female and 1 male, October 24, P. D. Hurd; 1 female, October 24, W. W. Wirth. 1950: 1 male, August 11, P. D. Hurd; 1 female, August 10, J. E. Gillaspy. 1951: 1 female, September 25, J. G. Rozen. 1953: 1 male, October 17. 1954: 1 male, August 15, H. E. and M. A. Evans; 2 females, October 14, A. M. Barnes; 1 female, October 14, M. Wasbauer; 5 females on *Lessingia glandulifera,* October 14, P. D. Hurd. 1955: 2 females, October 25, D. Burdick; 1 male, August 25, C. D. MacNeil. The holotype and allotype are in the collection of the University of California at Berkeley. Paratypes are with the holotype and in the collection of P. H. Timberlake, Riverside, California, the University of California at Davis, the California Academy of Sciences, San Francisco, the Snow Entomological Museum of the University of Kansas, Lawrence, Oregon State College at Corvallis, G. E. Bohart, Logan, Utah, the American Museum of Natural History, New York City, Cornell University at Ithaca, New York, J. G. Rozen at Ohio State College, Columbus, and in the author's collection.

Distribution. M. hurdi is known only from California (Fig. 28). In addition to the type material, 13 females and 2 males have been examined from the localities listed below (including the type locality).

California: Antioch; Oakley; Rio Vista; Turlock.

Flower Records. Artemisia sp., *Centromadia pungens, Eriogonum* sp., *Grindelia sp., G. camporum, Gutierrezia californica, Lessingia glandulifera, Solidago* sp.

Melissodes (Eumelissodes) pallidisignata Cockerell

Melissodes nigrosignata pallidisignata Cockerell, 1905, Proc. Biol. Soc. Washington, vol. 18, p. 180.
Melissodes menuacha vernonensis Viereck, 1905, Canadian Ent., vol. 37, p. 320 (new synonymy); Cockerell, 1906, Trans. Amer. Ent. Soc., vol. 32, pp. 77, 78; Cresson, 1928, Mem. Amer. Ent. Soc., vol. 5, p. 71.
Melissodes praelauta Cockerell, 1905, Psyche, vol. 12, p. 102 (new synonymy); 1906, Trans. Amer. Ent. Soc., vol. 32, pp. 75, 76; Snow, 1906, Trans. Kansas Acad. Sci., vol. 20, p. 137.

Melissodes pallidisignata is a highly variable species not closely related to any of the foregoing species. The females of *pallidisignata*

superficially resemble those of *menuachus, semilupina* and related species, but can be separated from these by the presence of dark brown hairs on the mesoscutum and scutellum. In the palest females only a few to several dark hairs occur medially on the scutellum, but usually they are abundant on the mesoscutum as well, and in the darkest females most thoracic hairs are black. The males of *pallidisignata* can be separated from those of *menuachus* and related species by the relatively short antennae. The antennae of *pallisdisignata* do not reach the prestigma in repose and the penultimate flagellar segment is always considerably shorter than three times its least diameter. In addition, the apices of the terga of the males are often infumate, varying from colorless to dark reddish brown, and dark hairs are often present on the scutellum and mesoscutum.

Female. Measurements and ratios: N, 20; length, 10-16 mm.; width, 3.5-5.0 mm.; wing length, $M = 3.84 \pm 0.269$ mm.; hooks in hamulus, $M = 14.85 \pm 0.182$; flagellar segment 1/segment 2, $M = 2.02 \pm 0.024$.

Structure and color: Integument black except as follows: apical half of mandible, lower surface of flagellar segments 3-10, distitarsi, and in pale forms apical halves of terga rufescent; eyes gray to grayish blue; wing membrane colorless, veins black to reddish brown (palest in eastern populations); tegulae dark reddish brown to black; tibial spurs pale yellow to pale brown.

Structure and sculpturing as in *agilis* except as follows: clypeus relatively flat, oculoclypeal distance equals less than two-thirds minimum first flagellar diameter, punctures round, irregular in size, separated by half to one puncture widths, surface moderately shiny to dull, with coarse shagreening relatively sparse to dense, supraclypeal area shiny to opaque and dulled by dense reticular shagreening; vertex with lateral flat areas moderately shiny, with small irregular punctures and usually slightly shagreened; galeae above shiny except at tips to completely dulled by dense, coarse tessellation; maxillary palpal segments in ratio of about 8:6:4:1, last two segments often longer, but third never longer than second. Mesoscutum with punctures on anterior third well separated, often by as much as one puncture width or more, posteromedian area often largely impunctate, when present punctures larger than anteriorly and separated by one to three puncture widths; scutellum punctures deep, round, mostly smaller than posterior mesoscutal and separated by one-half to two puncture widths; mesepisternal punctures shallow, often indistinct posterior borders, mostly as large as largest

mesoscutal, surface shiny and unshagreened to slightly and delicately so. Tergum 1 with basal three-fifths or less medially with punctures small, shallow, separated mostly by one puncture width or less, often with indistinct posterior margins, apical area impunctate, with large, oval, impunctate lateral areas extending anteriorly, surface dulled in punctate area by coarse, dense, reticulotransverse shagreening, an impunctate area shiny and shagreening extremely fine; tergum 2 with basal area punctures round, small, separated mostly by one puncture width, surface shiny, apical area impunctate and shagreening extremely fine, interband zone with scattered, irregular punctures, with lateral raised area punctures separated mostly by three puncture widths or more, surface shiny with sparse shagreening to dulled by dense, coarse, reticulotransverse shagreening; interband zone in addition to ordinary small punctures with large punctures having raised anterior rims giving rise to erect bristlelike hairs, these punctures also in apical part of basal area (other species have such punctures, but usually less conspicuous than in *pallidisignata* and usually not extending into basal area); tergum 3 similar but interband zone punctures more abundant; pygidial plate V-shaped with rounded apex.

Hair: Vestiture highly variable; palest specimens as in *ochraea* except as follows: scutellum with dark brown hairs; mesoscutum usually with posteromedian patch of dark hairs as large to twice as large as scutellar dark patch and often with pale hairs mixed with the dark anteriorly; vertex of head usually with several to many dark hairs; pale thoracic and head hairs usually pale ochraceous to white; tergum 2 with pale distal band notched medially along posterior border, not reaching apex of tergum at extreme sides except occasionally, interband zone hairs usually all pale, interband zone with long, bristlelike, erect hairs; tergum 3 similar to 2 but pale distal band often reaching apex laterally (rarely across lateral third or more), basal area with dark brown tomentum; tergum 4 with broad white apical pubescent band; terga 5 and 6 usually with pale lateral tufts; sternal hairs reddish brown except apically on sternum 5. Leg hairs pale ochraceous except as follows: inner surface hind and middle basitarsi, basitibial plate, fore basitarsus, and usually distitarsi dark brown; fore and middle tibiae often with outer apical surfaces pale brown. Considerable melanism occurs in various populations of *M. pallidisignata* and these melanistic specimens are described below under the topic of geographical variation.

Male. Measurements and ratios: N, 20; length 8-13 mm.; width, 2.5-4.0 mm.; wing length, M = 3.51 ± 0.262 mm.; hooks in hamulus,

M = 13.00 ± 0.178; flagellar segment 2/segment 1, M = 3.19 ± 0.089.

Structure and color: Integument black except as follows: clypeus yellow; labrum with small to large mediobasal pale spot; mandible with base black, with large triangular spot, or with small round pale spot; eyes green to bluish gray; flagellum yellow to red beneath (except first segment), reddish brown to black above; wing membrane colorless, veins red to dark brown, tegulae piceous; distitarsi rufescent; tibial spurs colorless to yellow; tergal apices colorless to dark reddish brown.

Clypeus relatively flat (as in *menuachus*); first flagellar segment minimum length about one-fourth to one-third maximum length second segment, often longer, penultimate segment more than one-third as broad as long (usually about two-fifths), flagellum in repose not reaching prestigma; maxillary palpal segments in ratio of about 3.5:2.5:2.5:1.0. Sculpturing as in female except as follows: clypeal punctures shallow; tergum 1 with basal four-fifths punctate, punctures often separated by more than one puncture width; interband zones of terga 2-4 usually more distinctly punctured and usually shinier than in female; sterna with surfaces shiny to dull, often with dense, coarse, reticular shagreening. Terminalia as in *rustica* described on following pages (Figs. 96-98).

Hair: Vestiture as in *menuachus* except as follows: scutellum often with a few to many dark hairs medially; mesoscutum frequently (especially in western populations) with abundant dark brown hairs on mesoscutum; dorsal thoracic hairs not usually appressed, long and loosely erect or short and erect; tegulae and vertex of head rarely with brown hairs. Metasomal terga 2-5 in dark specimens often with basal tomentum brown (not dark chocolate brown, but relatively pale brown as in milk-chocolate).

Geographical Variation. Melissodes pallidisignata is highly variable in several characters involving both sexes. This variation is at least partly geographic, and it would be possible to recognize from two to six (and possibly more) subspecies, depending upon which set of characters and upon which statistical criteria are used. In the present work subspecies are not recognized for reasons given below following the detailed account of the distribution of certain of the variable characters. First of all, both sexes are highly variable in regard to color of the vestiture. I shall discuss females first with regard to this and other characters. From the eastern border of the species range (see map, Fig. 24) west to central and southern California, central Oregon, Idaho, and southern British Columbia the

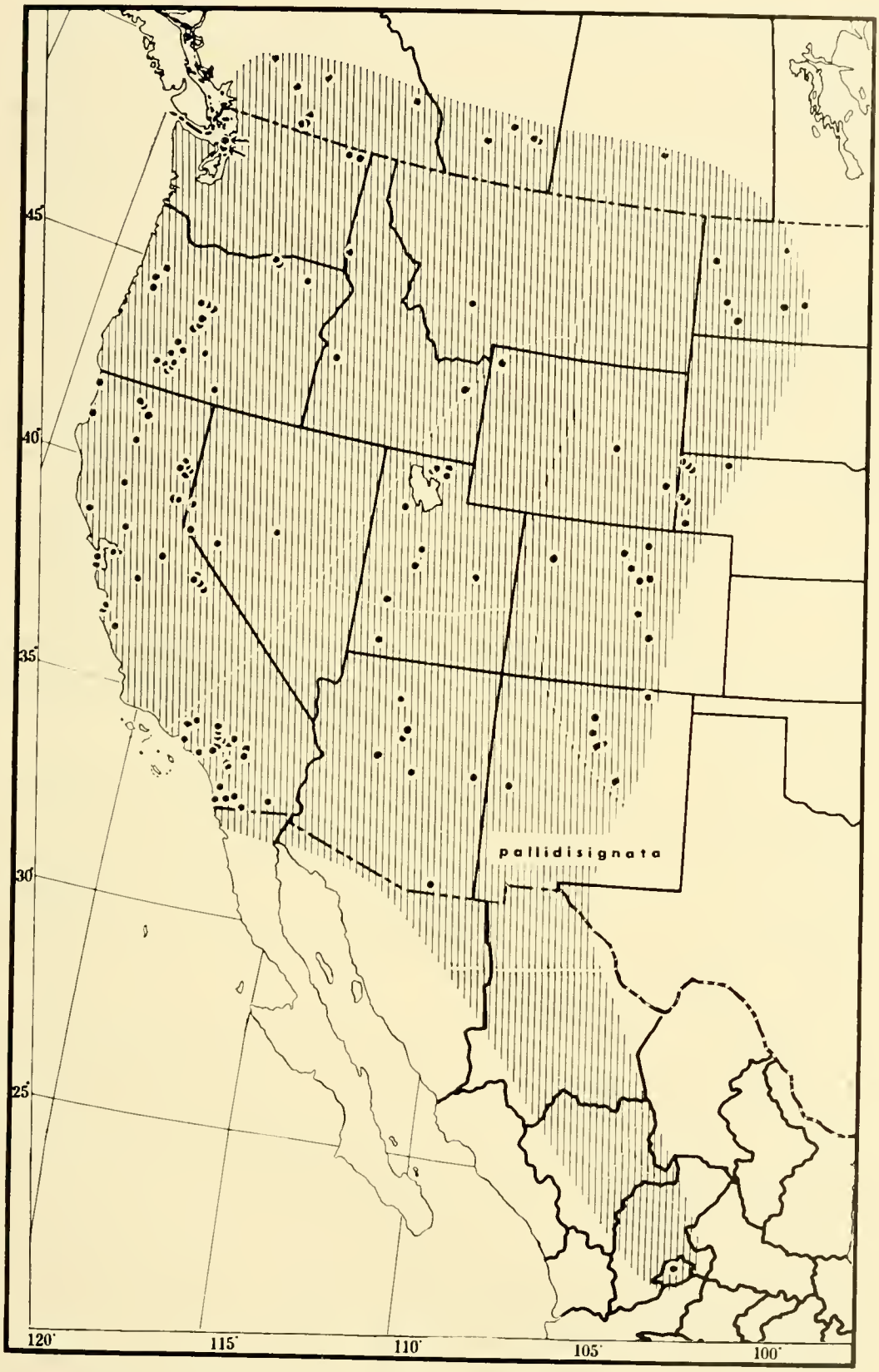


FIG. 24. Map showing the known distribution of *M. (Eumelissodes) pallidisignata* Cockerell.

females have a typically pale pattern with some local variations. In these females, the head hairs are usually all pale except brown on the vertex. The thoracic hairs are pale except medially on the scutellum and posteromedially on the mesoscutum where they are brown to black. The metasomal terga have pale pubescent bands as described in the formal description given above without any tendencies towards melanism.

In the populations of southern California (San Bernardino, Riverside, San Diego, and Mono counties) females show a strong tendency toward melanism of the vestiture of the mesoscutum and scutellum without showing any tendencies towards darkening of the metasomal, head or lateral thoracic hairs. This involves, especially, a progressive enlarging of the dark brown mesoscutal patch until in the darkest females this patch covers all of the mesoscutum except the extremely narrow anterior margin. The darkest females also have dark brown hairs on the posterior pronotal lobes. About 70-80% of the females from this area exhibit melanism of this type. This tendency occurs to a less marked degree in specimens from the inter-montane region (especially Utah) and in eastern Colorado and western Nebraska. In central and northeastern California, Idaho, British Columbia and Alberta this tendency is not evident.

The females from populations along the coast of California (north of northern Monterey County) in and west of the Coastal Range Mountains, north to Whidby Island, Washington and broadening eastward to include part of Siskiyou County in northern California, the western half of Oregon (especially the Crater Lake-Klamath Marsh area), and the Metaline Falls region of northeastern Washington exhibit a more extreme melanism. In these the mesepisternal hairs tend to become dark progressively from the ventral and anterior surfaces until in the darkest specimens the lateral surfaces of the thorax are entirely dark. The head hairs also are more melanistic than in the eastern form and, in the darkest, are entirely dark brown to black. The dorsum of the thorax, on the other hand, usually tends to remain as in the average eastern female with the mesoscutal dark patch remaining slightly larger than the scutellar dark patch and extending in area only in the darkest individuals. This is not so true, however, of the Metaline Falls, Washington population in which the mesoscutal patch enlarges concurrently with the darkening of the sides of the thorax and head. The metasomal terga also show melanism. Terga 5

and 6 lack pale lateral tufts in all but the palest females from this region. Tergum 4 tends to have the pale apical pubescent band partly or wholly dark brown. The pale distal bands of terga 2 and 3 tend to be dark medially. The long pale basal hairs of tergum 1 tend to be partly dark. The darkest of the females are from the Crater Lake-Klamath Marsh area of Oregon, the Metaline Falls area of Washington, and Mendocino, San Mateo and Monterey counties of California.

Using this set of female characters, three subspecies could be recognized, each occupying the ranges outlined in the preceding paragraphs. It should be emphasized here that the dark Southern California females differ from the dark coastal females not only in intensity of melanism, but also in the pattern of melanism. It is this sort of difference (that is, pattern rather than degree) which the author has used to help in distinguishing species in this genus and, furthermore, some melanism patterns are typical of certain subgenera.

Along with the melanism pattern described above, there is variation in the length of the hair, particularly of the head and thorax. The eastern form usually has short hairs which on the dorsum of the thorax has a peculiar clipped appearance when viewed under a stereoscope. The dark coastal females have exceedingly long, loose hairs, not at all appearing clipped on the thorax. However, the Crater Lake-Klamath Marsh area of Oregon, where some of the darkest females occur, has females with hairs of short to medium length and usually with clipped appearance. The females from the Metaline Falls area of Washington have very short, clipped hairs. These last are also among the darkest of the females.

Pale females in a long series from Antioch and Oakley (Contra Costa County) and Turlock (Stanislaus County) in California have the hair short to medium (medium especially in the Antioch females) in length. These populations are very near in space to populations of typical long-haired, dark females in San Mateo and Monterey Counties, so that some intermediates in hair length might be expected to occur here. Intermediates in hair color ought also to occur in the Antioch-Turlock area and some do. In this area females lack the tendency towards enlargement of the mesoscutal dark patch beyond the average size of this patch of the eastern populations. Also, a small number of females from Antioch have a few to several brown hairs on the ventral surfaces of the mesepisterna and lack pale lateral tufts on terga 6 and 7. However, the Antioch-Tur-

lock populations also include the palest females known in this species (especially in the series from Turlock). In these pale individuals the mesoscutal hairs are entirely pale ochraceous and only a few to several dark brown hairs are present on the scutellum. It seems as if very little migration and gene flow occurs across the southern San Francisco Bay area and across the Coastal Range Mountains in this area, or the selective forces operating in the two areas are especially effective. Also, there seems to be rather limited gene flow between the Antioch-Turlock populations and the southern California populations, but there is a large gap in central California from which no specimens are available.

Populations of the Metaline Falls region of northeastern Washington are also peculiar in that the females average dark in color (although less so than in the Crater Lake-Klamath Marsh area of Oregon) and have exceedingly short, clipped hairs on the thorax. This population includes some of the darkest females known. Also, the tendency towards expansion of the mesoscutal dark patch occurs here even in relatively pale females, much as in southern California. Furthermore, females in these populations tend to have the mesoscutal hairs (especially anterior to the dark patch) pale rufescent rather than pale ochraceous or white. This is similar to the related, more eastern species, *Melissodes rustica* (Say). A fourth subspecies could possibly be recognized in this area using the combination of characters outlined in this paragraph.

Southern British Columbia females are similar to those of the Antioch-Turlock area in that there is some darkening of the ventral mesepisternal hair. Otherwise these females are typical of the more eastern populations in color and hair form.

In addition to these characters, the sculpturing of the galeae and of the metasomal terga (base of tergum 1 and interband zones of terga 2 and 3) is variable. The distribution of these characters follows that of hair color to some extent, but there is more intrapopulational variation and certain exceptional areas where the correspondence between hair color and sculpturing does not hold. In general the pale populations have shiny, unshagreened (except at tips) galeae and shiny, finely shagreened interband zones of tergum 2, whereas the darker populations have densely shagreened, opaque galeae (or at least the apical half or more of the galeae are shagreened) and densely shagreened, dulled interband zone of tergum 2.

Females of the populations of southern California and eastern California east of the southern Sierra Nevada Mountains consistently

have the shinest galeae and terga. Females from the Turlock area are similar. From the Antioch area, however, the females appear intermediate in this respect, about 50% having dull and 50% having shiny galeae and second terga. From nearby San Mateo and Monterey counties the females have dull galeae and terga. In Oregon, the females, whether pale or dark, are a mixture similar to that of the Antioch area in regard to sculpturing, but tend more towards greater shagreening of both galeae and second terga. The dark females from the Metaline Falls area of Washington consistently have densely shagreened galeae and second terga. Females from southern British Columbia are somewhat intermediate, but show a high degree of shagreening (70% or more dulled). The females of the populations to the east of these areas generally are intermediate in sculpturing of the galeae and terga, but more often have shiny galeae and dulled second terga than otherwise.

The size of the individuals (both male and female) is also variable. However, for the most part there seems to be no consistent geographical pattern in size variation. In general this is a medium-sized to large bee. The populations from the desert areas of southern California (excluding Los Angeles and Kern counties) appear to have consistently smaller individuals than elsewhere in the range. Also, specimens from the Crater Lake-Klamath Marsh area of Oregon seem to average smaller than normal, but not as small as the southern California specimens.

From the foregoing, which is based on female characters alone (except for size variation), four or five more or less well-marked subspecies can be recognized. The first consists of dark, long-haired females with dulled galeae and second terga occupying the coastal region of California north of Monterey County, Oregon and Washington (and perhaps southern British Columbia). The second consists of populations of southern California north to Los Angeles in the west and Mono County in the east in which females are small, short-haired, have shiny galeae and second terga and tend to have the mesoscutal dark patch much enlarged. The third consists of dark females with dark mesoscutal hairs, dulled galeae and second terga, somewhat rufescent mesoscutal pale hairs, and short hair occupying the Metaline Falls region of northeastern Washington. The rest of the range of the species in central and eastern California, eastern Oregon, Southern British Columbia, and states and provinces to the east is occupied by the fourth form in which females are short-haired, of medium melanism, and usually with shiny

galeae and second terga. The last would be a poorly marked subspecies, as in each characteristic it falls somewhat in between two or more of the other subspecies. A fifth form might also be recognized occupying the central valley (Turlock) area of California, as females from this area are consistently paler than from elsewhere in the range of the species.

The males have a few characteristics which vary geographically and which do not apply to the females. The first of these concerns mandibular color. The base of the mandible is either black, has a small round yellow spot, or has a large triangular yellow macula. These three states can be considered as two extremes and the intermediate condition of one character. Males from Alberta, Saskatchewan, North Dakota, eastern Wyoming, Nebraska, Colorado, Utah, Arizona and New Mexico usually have mandibles with large yellow maculae at their bases. Occasional specimens (5% or less) have small round yellow spots. None from this area has black mandibular bases. Populations from Utah bear the highest proportion of males with small round mandibular yellow spots (3 out of only 10 males known from Utah) and seem to be intermediate populations in this respect, but the samples are small. To the west of this area males usually have the base of the mandible black, but rare individuals with the intermediate condition occur in almost every population from which reasonable sized samples are available. For instance, from Oregon 115 males were examined and seven had the intermediate condition (slightly less than 6%), the remaining 108 had black mandibular bases. Nine males were available from northwestern Wyoming (Yellowstone National Park) and of these two had small mandibular spots, the remaining seven black mandibular bases. This population could be also considered as intermediate, although the sample is small. Consideration of this male character splits the eastern populations (fourth subspecies of the preceding paragraph) almost equally into two large areas and a fifth (or sixth) subspecies could be thus recognized in the eastern-most and southeastern parts of the species range. This subspecies would be characterized primarily by the males having large, yellow, triangular maculae on the mandibular bases.

Another male characteristic which varies a good deal is the integumental color of the apices of the terga. This varies from colorless through yellow and pale brown to brown or dark brown. Specimens from the same populations in which males have large triangular yellow mandibular maculae usually have colorless or yellow

tergal apices. To the west the males usually have pale to dark brown tergal apices, with considerable intrapopulational variation. However, the central California populations from Riverside to Antioch have almost all males with colorless or yellow terga, so this character could be used in conjunction with the pale color of the females to delimit a subspecies. However, the distribution of this character, especially in central California, does not follow the distribution of other characters very closely. Except for this character, the Riverside population falls within the southern California desert form. Likewise, the Antioch area does not seem to be transitional to the dark coastal form in this character as it is in certain female characters discussed above.

As to size and sculpturing, what has been said concerning the females applies generally to the males. However, the males appear to have considerably more intrapopulational variation with respect to these characteristics and they would scarcely be useful in delimiting subspecies. This is also true of hair color. Males in general are much paler than the females from the same area and there is a large amount of intrapopulational variation among males in regard to hair color. It is interesting to note, however, that the darkest males are from the Crater Lake-Klamath Marsh area of Oregon and the males from this area average darker than from the coastal area of California, Oregon and Washington. The hair length, particularly of the head and thorax, of the males is distributed about as it is in the females.

It is evident from the foregoing, sketchy as the data may be, that first, there are a number of characters varying in a clinal fashion. Second, the clines of these characters are correlated with one another in some areas but not in others. Third, characters not clinally distributed are also present. Fourth, no one of the eight characters discussed (3 female and 5 male) is distributed precisely like any one other with the same breaks in distribution, whether clinal in nature or not (the only possible exception to this occurs between characters which apply to both females and males, such as sculpturing or hair length). Some characters may coincide with others in being limited by the same boundary in some parts of the range (hair color and hair length in females coincide in the San Mateo-Monterey area and the Antioch-Turlock area of California) but not in other areas (hair color and hair length do not coincide in distribution in Oregon and Washington). In the foregoing I have tried to distinguish between the correlation in direction of clinal

characters and the coincidence of the break in the distribution of characters.

Although combinations of characters could be used to classify these sampled populations, it seems evident to the writer that to do so would be to represent the facts in an artificial manner and, indeed, would tend to obscure the actual distribution of the characters which is exceedingly complicated. An arbitrary decision would first have to be arrived at as to which characters to use and which to ignore. Another arbitrary decision would have to be made as to what percent of which sex must be identifiable in order to limit the range of each race. Also, some subspecies would be characterized by female and others by male characters alone, or characters pertaining to one or the other sex would have to be ignored.

If six subspecies were recognized using all characters studied, many of the populations from which samples are available would be classified as intermediate populations between two or more subspecies. This would be an error in the light of the facts of the distribution of the characters. The so-called intermediate populations are, in fact, simply populations exhibiting combinations of characters differing from the nearby populations classified as subspecies. Yet the populations classified as subspecies and not intermediates are distinctive for the very same reason. That is, they possess a peculiar combination of characters. Both types of populations have these distinctive combinations because of the character clines and/or the distributions of characters not being well-correlated or not coinciding in area. Which populations represent subspecies proper and which represent intermediates or intergrades then depends upon the viewpoint of the observer. That is, it depends upon which characters he selects as being important in delimiting and classifying the geographical races. The facts indicate that almost every geographic area from which a large enough sample is available is occupied by a population made distinctive by a peculiar combination of characters.

In view of this situation the author regards the recognition of subspecies as being superfluous or even scientifically in error. In cases where only one or two characters in a species are known to vary geographically, it may be desirable from a pragmatic point of view to recognize two or more subspecies. Also, if many characters are varying, it may be possible to recognize races by using some of the more subtle multivariate statistical procedures. However, the author knows of no good example of such an analysis in entomo-

logical work, and the results obtained thereby would be subject to the same objections reviewed in the preceding paragraphs.

A statistical or graphical representation of the facts in *M. pallidisignata* was not prepared for the reason that, although several hundred specimens were available for study, they were not distributed in such a manner as to provide good samples from most areas. For instance, out of approximately 700 specimens available, over 400 were from six localities or limited areas, with less than 300 distributed unevenly over the remaining range of the species. A statistical, and even a graphical, representation could have been very misleading.

Bionomics. Table XIII gives a summary of the available flower records from field collections for *M. pallidisignata.* These data indicate that *pallidisignata* is an oligolege of the family Compositae and depends primarily upon flowers of the genera *Isocoma, Chrysothamnus,* and *Grindelia* in that order of preference.

Type Material. Female holotype of *pallidisignata* Cockerell collected by F. H. Snow in August at Oak Creek Canyon, Arizona, is in the Snow Entomological Museum of the University of Kansas, Lawrence. Female holotype and male allotype of *vernonensis*

TABLE XIII. Summary of Floral Records for *Melissodes pallidisignata.*

Plant Data			Records of *M. pallidisignata*			
FAMILY	Number of genera	Approximate number of species	Number of collections	Number of females	Number of males	Total number of bees
Compositae:						
Isocoma spp.	1	2	30	42	26	68
Chrysothamnus spp.	1	2	17	33	27	60
Grindelia spp.	1	3	15	18	33	51
Solidago spp.	1	3	12	6	51	57
Gutierrezia spp.	1	2	7	6	10	16
Other genera	15	17	32	26	19	45
Other families (2)	6	6	18	13	23	36
Totals	26	35	131	144	189	333

Viereck from Vernon, British Columbia, August 17, 1904, are in the collection of the Philadelphia Academy of Sciences. Male holotype of *praelauta* Cockerell collected by F. H. Snow in July at Oak Creek Canyon, Arizona, is in the Snow Entomological Museum (this male unlike other Arizona males examined by the author, has black mandibular bases, otherwise it is like the pale New Mexico, Colorado, Arizona and Nebraska males).

Distribution. From southern California to southern British Columbia in the west, to southern Saskatchewan, western North Dakota and Nebraska, eastern Colorado and New Mexico in the east (Fig. 24). A single female from the state of Agauscalientes in Mexico is assigned to this species and the range presumably extends that far south, although no other specimens have been seen from Mexico. This species has been collected from June 10 to October 27, but chiefly in August. In addition to the type specimens, 333 females and 523 males have been examined from the localities listed below (including localities reported in the literature).

ARIZONA: Apache Co.; East Verde River; Flagstaff; Grand Canyon (South Rim); Huachuca Mts.; Oak Creek Canyon; Prescott. CALIFORNIA: Anaheim; Antioch; Arcata, Humboldt Co.; Artois; Bridge Creek Camp, Lassen Co.; Cloverdale; Convict Lake, Mono Co.; Crescent City; Davis; Elk Creek, Siskiyou Co.; Erwin Lake, San Bernardino Co.; Grant Lake, Mono Co.; Greenfield (8 miles W.); Helendale; Hemet Valley, San Jacinto Mts.; Imperial Co.; Inglenook Swamp, Mendocino Co.; Jacumba; Mt. Laguna; Lancaster; Litchfield; Los Angeles; Los Angeles Co.; Mammoth; McCloud; Milford; Millbrae; Mission Valley; Mono Lake, Mono Co.; Morongo Valley; Moss Beach, San Mateo Co.; Naples; Oakley; Old Shasta; Oro Grande; Pacific Grove; Pine Knot, Bear Lake, San Bernardino Co.; Pine Meadow, San Jacinto Mts.; Pinos, Monterey Co.; Redlands; Riverside; San Diego; San Diego Co.; San Felipe Creek, S. Diego Co.; Sierraville; Sisson, Siskiyou Co.; Standish (and 4 miles W.); Tesla; Turlock; Upper Santa Ana River, S. Bernardino Co.; Vallecito; Victorville; Whitewater; Yuba Pass, Sierra Co. COLORADO: Berkeley; Boulder; Boxelder Creek (E. of Aurora); Colorado Springs (Fountain Valley School); Denver; Eaton; Estes Park; Meeker; Medicine Bow; Pueblo. IDAHO: Emmett (10 miles E. at Squaw Creek); Lewiston; Rexburg. MONTANA: Whitehall. NEBRASKA: Gering; Glen, Sioux Co.; Gordon; Kimball; Mitchell; Monroe Canyon, Sioux Co.; War Bonnet Canyon, Sioux Co. NEVADA: Austin; Minden; Reno; Walker Lake. NEW MEXICO: Embudo (6 miles N. E.); Omega; Raton; Rowe; Santa Fe (and 12 miles S. E.);

Vaughn. North Dakota: Bismarck; Denbigh, McHenry Co.; Dickinson; Mott; Schafer; Steele. Oregon: Bend (20 miles S. and at Sandy River S. of); Chemult; Crater-Diamond Lake Road Junction, Klamath Co.; Crater Lake Park (East Entrance; Lost Creek; near Headquarters; Pole Bridge Meadows; 8 miles out on Medford road); Corvallis; Echo; Fort Klamath (and 5 miles N.); Klamath Falls (54 miles E. and 59 miles N.); Klamath Marsh; LaGrande (5 miles N.); Lapine; Prineville (10 miles W.); Salem-Albany road; Silver Lake; Sisters (and 14 miles E.); Umatilla; Willamette River. Utah: Bert; Cande; Delta; Emery Co.; Jericho; Milford; Petersboro; Promontory; Thatcher; The Dalles; Zion Park. Washington: Coupeville (Whidby Island); Metaline Falls; Northport; Whidby Island. Wyoming: Casper (E. at 10 mile draw); Lingle; Yellowstone National Park. *Canada.* Alberta: Lethbridge; Medicine Hat; Redcliffe; Scandia. British Columbia: Invermere; Lillooet; Nicola; Oliver; Penticton; Similkameen (towards Okanagana); Vernon; Walhackin. Saskatchewan: Caron. *México.* Aguascalientes: Rincon de Romos (12 km. N.).

Flower Records. Aplopappus sp., *A. gracilis, Aster* sp., *A. adscendus delectabilis, Centromadia pungens, Chrysopsis hispida, Chrysothamnus* sp., *C. nauseosus, C. n. mojavensis, C. n. occidentalis, C. n. viscidiflorus, Cirsium* sp., *Cleome* sp., *C. serrulata, Ericameria palmeri, Grindelia* sp., *G. camporum, G. platyphylla, G. squarrosa, Gutierrezia californica, G. sarothrae, Helianthus* sp., *Heliotropium* sp., *Hemizonia* sp., *Heterotheca grandiflorum, Isocoma acradenia, I. vernoniodes, Lepachys* sp., *Lessingia glandifera, Medicago sativa, Melilotus* sp., *M. alba, Petalostemum* sp., *P. occidentalis, Pluchea persica, Psilostrophe gnaphalodes, Senecio ionophyllus, Solidago* sp., *S. canadensis, Wislizenia refracta.*

Melissodes (Eumelissodes) rustica (Say)

Macrocera rustica Say, 1837, Boston Jour. Nat. Hist., vol. 1, p. 406; LeConte, 1859, Entom. Writ. Th. Say, vol. 2, p. 781.

Melissodes rustica, Smith, 1854, Cat. Hymen. Brit. Mus., vol. 2, p. 309; Cresson, 1879, Trans. Amer. Ent. Soc., vol. 7, p. 225; Patton, 1879, Bull. U. S. Geol. Surv., vol. 5, p. 472; Provancher, 1888, Addit. Pet. Faun. Canada, Hymen., vol. 2, p. 300; Evans, 1896, Can. Ent., vol. 28, p. 13; Birkman, 1899, Ent. News, vol. 14, p. 245; Bridwell, 1899, Trans. Kansas Acad. Sci., vol. 16, p. 211; Viereck, 1903, Ent. News, vol. 14, p. 119; Smith, 1910, Ann. Rep. New Jersey State Mus., 1909, p. 693; Graenicher, 1911, Bull. Pub. Mus. Milwaukee, vol. 1, p. 247; Viereck, 1916, Bull. Connecticut Geol. Nat. Hist. Surv., vol. 22, p. 732; Graenicher, 1935, Ann. Ent. Soc. Amer., vol. 28, p. 304; Proctor, 1938, Biol. Surv. Mt. Desert Region, vol. 6, p. 444; Brimley, 1938, Insects of North Carolina, p. 463.

Melissodes assimilis Smith, 1879, Descr. of new species of Hymen. in the collection of the British Museum, p. 114 (new synonymy).

Melissodes ambigua Smith, 1879, Descr. of new species of Hymen. in the collection of the British Museum, p. 116 (new synonymy).
Melissodes festinata Provancher, 1888, Addit. Pet. Faun. Canada, Hymen., vol. 2, p. 300 (new synonymy).
Melissodes simillima Robertson, 1897, Trans. Acad. Sci. St. Louis, vol. 7, p. 355; 1905, Trans. Amer. Ent. Soc., vol. 31, p. 368; Cockerell, 1906, Trans. Amer. Ent. Soc., vol. 32, p. 113; Lovell and Cockerell, 1906, Psyche, vol. 13, p. 111; Robertson, 1918, Ent. News, vol. 25, p. 70; Viereck, 1916, Bull. Connecticut Geol. Nat. Hist. Surv., vol. 22, p. 732; Pearson, 1933, Ecol. Monogr., vol. 3, p. 381; Robertson, 1926, Ecology, vol. 7, p. 380; 1928, Flowers and Insects, p. 8; Brimley, 1938, Insects of North Carolina, p. 463.
Melissodes asteris Robertson, 1914, Ent. News, vol. 25, p. 70 (new synonymy); 1914, Ent. News, vol. 25, p. 373; 1926, Ecology, vol. 7, p. 379; 1928, Flowers and Insects, p. 8; Michener, 1947, Amer. Mid. Nat., vol. 38, p. 454.

Melissodes rustica is a small, highly variable species closely allied to *M. pallidisignata* Cockerell. It differs from the latter chiefly in its smaller size and generally darker color. Females of *rustica* are difficult to distinguish from those of *pallidisignata* because of the large amount of color variation exhibited in both species. Females of *rustica* can be characterized as follows: mesoscutum always with brown patch of hairs at least as large as scutellar dark patch; mesepisterna usually with dark hairs at least below; tergum 2 with punctures not of two conspicuously different sizes as in *pallidisignata;* scopal hairs usually yellow; apical areas of terga 1-3 impunctate, shiny, apubescent or almost so and distal pale pubescent bands of terga 2 and 3 not reaching apices of terga at sides. The males of *rustica* differ from those of *pallidisignata* as follows: dark reddish brown tergal apices; mandibular bases black; labrum usually with pale mediobasal spot; first flagellar segment with minimum length one-sixth to one-fourth maximum length of second segment, flagellum reaching or surpassing pterostigma in repose. In addition, the male of *rustica* has the punctation of tergum 2 as in the female.

Female. Measurements and ratios: N, 20; length, 10.0-14.5 mm.; width, 3.0-4.5 mm.; wing length $M = 3.37 \pm 0.126$ mm.; hooks in hamulus, $M = 12.55 \pm 0.256$; flagellar segemnt 1/segment 2, $M = 1.91 \pm 0.024$.

Structure and color: Integument black except as follows: apical half of mandible, lower surface flagellar segments 3-10, and usually distitarsi rufescent; terga 1-3 with apical areas dark reddish brown to black; eyes gray to greenish blue; wing membranes slightly infumate, veins dark brown to black; tegulae piceous; tibial spurs white to yellow, occasionally brown along serrated margins.

Structure and sculpturing as in *pallidisignata* with the following differences: clypeus with punctures usually more crowded and slightly larger, surface shagreening coarse, dense, dulling surface;

supraclypeal area usually dulled by sparse, shallow punctures and sparse, reticular shagreening; galeae usually dulled above in apical half or more; maxillary palpal segments in ratio of about 3.5:3.0: 2.5:1.0, rarely with minute fifth segment present. Mesoscutum with punctures of anterior third crowded, mostly separated by half a puncture width or less, posteromedian area with punctures sparse, separated mostly by one to three puncture widths; scutellum with medial punctures separated by less than one to two puncture widths; mesepisternum with surface and bottoms of shallow punctures usually dulled by irregular, fine shagreening. Tergum 2 with basal area punctures small, round, separated by one to two puncture widths, surface dulled by fine reticular shagreening, interband zone punctures small, irregular, scattered, separated mostly by two to three puncture widths, surface dulled by coarse, reticular shagreening, without conspicuous large punctures at bases of bristlelike hairs, apical area impunctate, extremely shiny, with extremely fine reticulotransverse shagreening; tergum 3 similar to tergum 2 but basal area and interband punctures more crowded and apical area often with scattered minute punctures.

Hair: Vestiture highly variable; palest forms as follows: head white to ochraceous except brown on vertex; thorax white to ochraceous, often pale rufescent anteriorly on mesoscutum, scutellum with abundant dark brown and mesoscutal dark patch as large or larger than scutellar dark patch; metasomal tergum 1 with pale ochraceous hairs anteriorly, with ochraceous to yellow on basal three-fifths or more; tergum 2 with basal pubescence white to pale ochraceous, interband zone hairs suberect and mostly black, distal pale pubescent band ochraceous to yellow and usually narrowly interrupted medially, apical area often with sparse, short, subappressed hairs laterally near pale distal band; tergum 3 similar but basal tomentum thick, dark brown and distal band not interrupted, distal bands of terga 2 and 3 not reaching apices of terga laterally; tergum 4 with apical pale band uninterrupted medially, narrower than basal dark area; terga 5 and 6 often with small lateral pale tufts; sterna brown; legs pale ochraceous except as follows: scopae usually yellow, basitibial plate brown, fore and middle tarsi, outer surfaces fore and middle tibiae, inner surfaces hind basitarsi and tibiae and occasionally upper surface hind femora dark brown. In darkest females all hair dark brown to black except yellow scopal hairs and a few pale hairs at margins of posterior pronotal lobes, mesoscutum and wing bases. The variation is discussed in detail below in the section on geographical variation.

Male. Measurements and ratios: N, 20; length, 7.5-11.5 mm.; width, 2.0-3.0 mm.; wing length, M = 3.12 ± 0.163 mm.; hooks in hamulus M = 11.55 ± 0.223; flagellar segment 2/segment 1, M = 5.31 ± 0.083.

Structure and color: Integument black except as follows: clypeus yellow with brown or rufescent apical margin: labrum with pale mediobasal spot; apical half of mandible and distitarsi rufescent, mandibles without basal yellow spots; terga with apical areas reddish brown; eyes yellowish green to bluish green or gray; wings, tegulae and tibial spurs as in female, but wing membranes often colorless and veins often reddish brown.

Structure as in *pallidisignata* except as follows: first flagellar segment minimum length one-fourth to one-sixth maximum length of second segment, penultimate segment one-third as broad as long or slightly shorter, in repose flagellum reaches pterostigma or slightly beyond; maxillary palpal segments in ratio of about 3.0:3.5:3.0:1.0, first segment occasionally almost as long as second and rarely minute fifth segment present. Sculpturing as in female except as follows: clypeal punctures shallow; galeae often unshagreened except in apical third; mesoscutum with posteromedian punctures usually sparser; tergum 1 with basal four-fifths with punctures separated by one-half to two puncture widths; tergum 2 with basal area punctures separated by one to three puncture widths, surface more finely shagreened; terga 3 and 4 with interband zone with coarse, reticular shagreening appearing almost like tessellation and completely dulling surfaces. Sternum 7 as in *agilis.* Sternum 8 as in *agilis* but apical hairs long and abundant, medioventral tubercle not bidentate, pointed. Genital capsule as in *agilis* but gonostyli with hairs sparse and short.

Hair: Vestiture as in *pallidisignata* and *menuachus* except as follows: pale hairs usually pale ochraceous to yellow; vertex of head usually with at least a few brown hairs; scutellum and mesoscutum often with brown hairs; tegulae often with brown hairs; tergum 2 with interband zone hairs suberect, partly or wholly dark brown; terga 3-5 with basal tomentum dark chocolate brown; terga 6 and 7 dark brown and usually without pale lateral tufts; tergum 5 often lacking pale distal band and tergum 4 with pale band often interrupted medially; sterna brown except laterally; legs pale ochraceous except as follows: middle and hind basitarsi yellow to reddish brown on inner surfaces, basitibial plates often pale brown.

Geographical Variation. The females of *rustica* are highly variable in regard to vestiture color. This variation is distributed

geographically. The males follow this variation in color, but are never as dark in color as the females and usually show much more intrapopulational variation. For this reason the following account is based upon the variation in females only.

The collections of the females of this species are abundant enough and so distributed as to make a graphical representation of the color variation feasible. Females were grouped geographically and classified into three states each of eight characters of vestiture color. The characteristics are listed below, each with the three states in the order of increasing melanism.

1. Tergum 4, distal pale pubescent band:
   a. Without brown pubescence medially.
   b. Brown pubescence apicomedially to 50 percent brown.
   c. More than 50 percent brown to entirely brown.
2. Tergum 3, distal pale pubescent band:
   a. Not interrupted medially.
   b. Interrupted medially up to one-third width of tergum.
   c. Interrupted medially by one-third width of tergum to entirely dark brown.
3. Tergum 2, distal pale pubescent band:
   a. Narrowly interrupted medially (less than one-fifth width of tergum).
   b. Broadly interrupted medially (by one-fifth to one-half width of tergum).
   c. Interrupted medially by one-half width of tergum to entirely dark brown.
4. Tergum 1, hairs of anterior surface:
   a. Entirely pale.
   b. From a few to 50 percent dark brown.
   c. More than 50 percent to entirely dark brown.
5. Mesoscutal dark hair patch:
   a. Not extending forward to a transverse line at anterior margins of tegulae; with abundant pale hairs mesad of tegulae; pronotal hairs pale.
   b. Extending forward to or beyond a transverse line at anterior margins of tegulae; with few or no dark hairs mesad of tegulae; pronotal hairs all or mostly pale.
   c. Extending forward almost or quite to pronotum medially; without pale hairs mesad of tegulae; pronotal hairs mostly or all dark.
6. Mesepisternal hairs:
   a. All pale (except a few pale brown ventrally).
   b. Brown on ventral and anterior surfaces and on lower lateral surface (less than 50 percent of lateral surface).
   c. Dark brown on 50 percent or more of lateral surfaces.
7. Head hairs:
   a. Pale except vertex with abundant dark hairs.
   b. Vertex, labrum and clypeus with dark brown hairs, but clypeal hairs partly to almost entirely pale.
   c. Vertex, labral and clypeal hairs entirely dark brown; other head hairs partly to entirely dark brown.

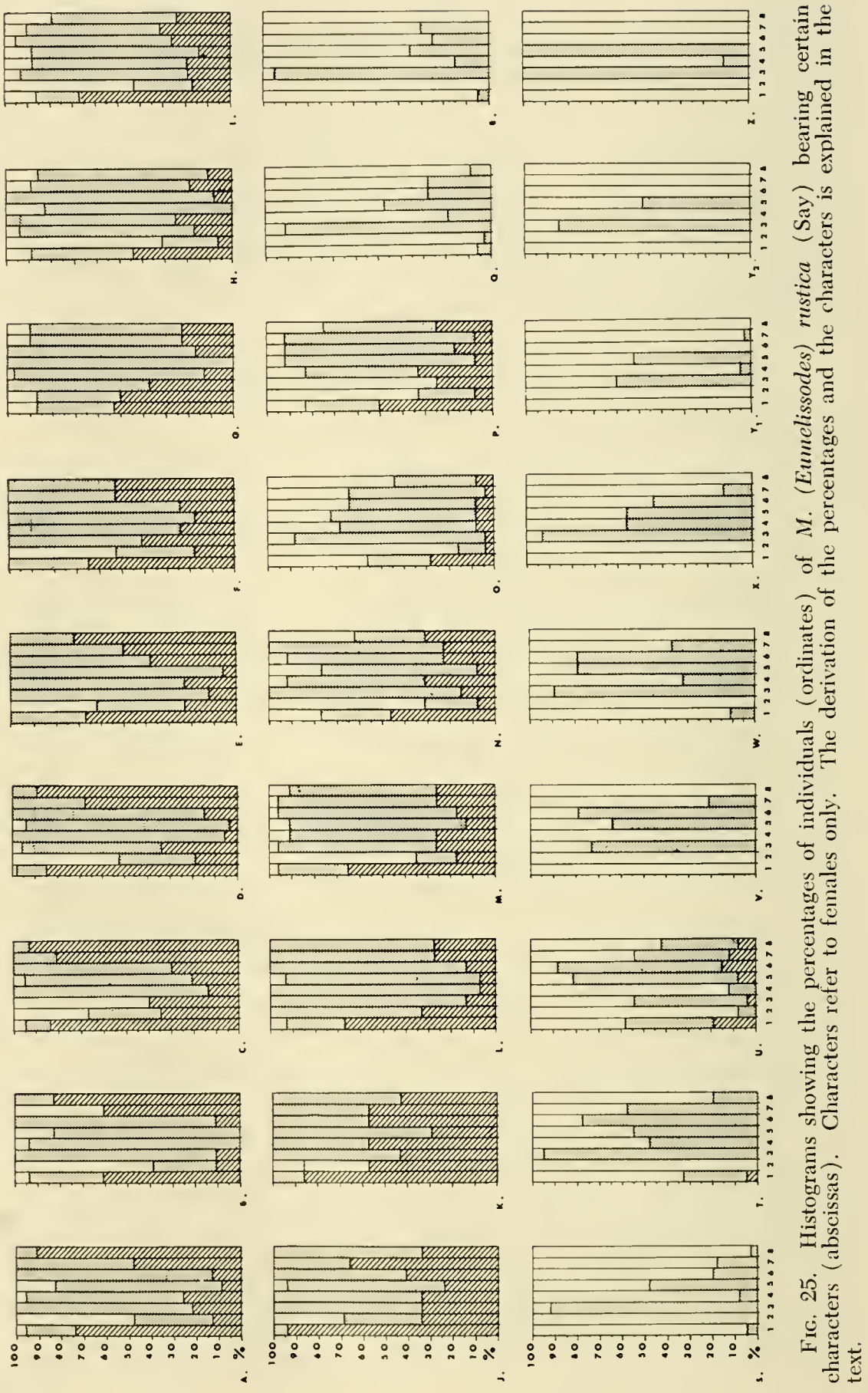


FIG. 25. Histograms showing the percentages of individuals (ordinates) of *M. (Eumelissodes) rustica* (Say) bearing certain characters (abscissas). Characters refer to females only. The derivation of the percentages and the characters is explained in the text.

8. Leg hairs:
   a. Coxae, trochanters, femora and outer surfaces of tibiae mostly pale.
   b. Tibiae, coxae, trochanters and inner surfaces of femora brown; outer surfaces of femora partly brown.
   c. All dark brown to black except scopae and occasionally anterior surfaces of femora.

After females from each of the geographical areas were classified according to the above characters, percentages of females exhibiting each state of each character for each geographical area were calculated and these percentages were used to prepare bar graphs (Fig. 25). The graphs are arranged roughly from North to South and from East to West. The numbers of females examined from each area are given below each graph together with the letter corresponding to the lettered list given below and to the lettered areas indicated on the distribution map (Fig 27). A—New Brunswick, Nova Scotia, Maine; B—Vermont, New Hampshire; C—Massachusetts, Connecticut, Rhode Island; D—New York; E—New Jersey; F—Pennsylvania; G—Maryland, District of Columbia; H—Virginia; I—North Carolina; J—South Carolina, Georgia; K—Alabama, Mississippi, Louisiana; L—Quebec, Ontario; M—Ohio, Indiana, West

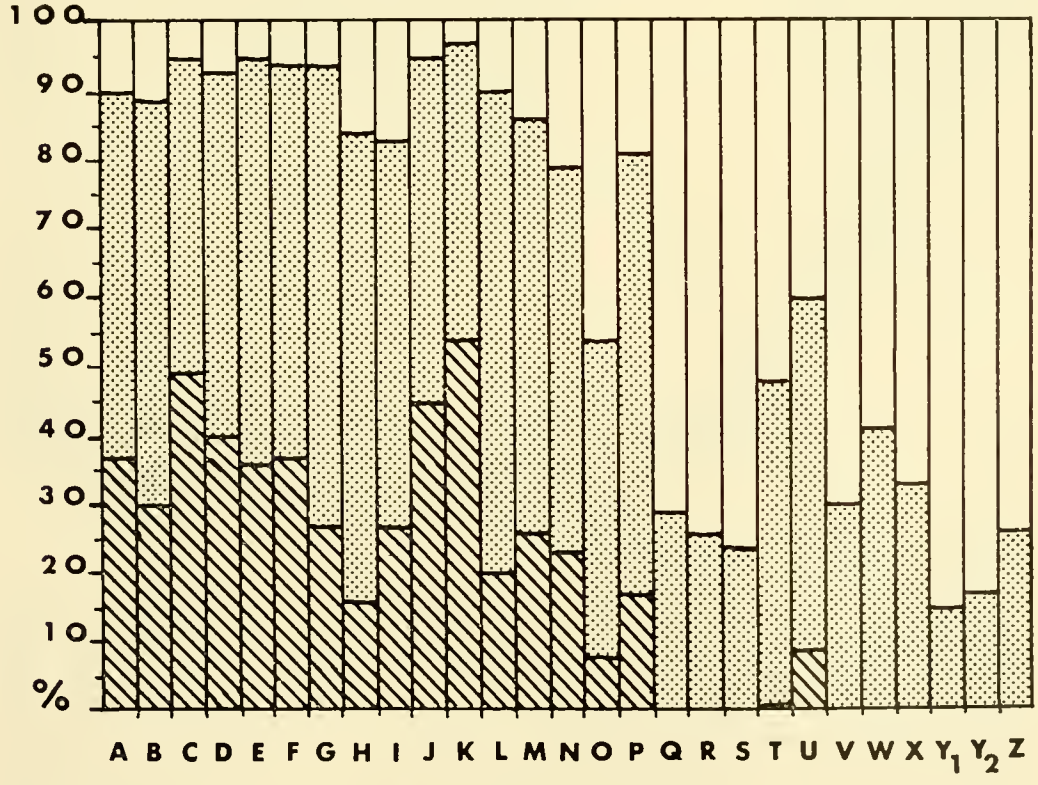


FIG. 26. Histogram for *M. (Eumelissodes) rustica* (Say) showing the average percentage (ordinate) for females within each of several localities (abscissa). The derivation of these percentages and location of the lettered localities is explained in the text.

Virginia; N—Wisconsin, Michigan; O—Illinois; P—Iowa, Missouri; Q—Minnesota; R—Manitoba; S—North Dakota; T—Nebraska (Lincoln); U—Kansas; V—Saskatchewan, Idaho, Montana, Wyoming; W—Colorado, New Mexico; X—Utah; Y1—Northern Arizona; Y2—Central Arizona; Z—Durango, Mexico. The three states of each of the eight characters were added together and averaged to obtain a melanism factor for each of the twenty-seven localities. These are illustrated in a bar graph (Fig. 26).

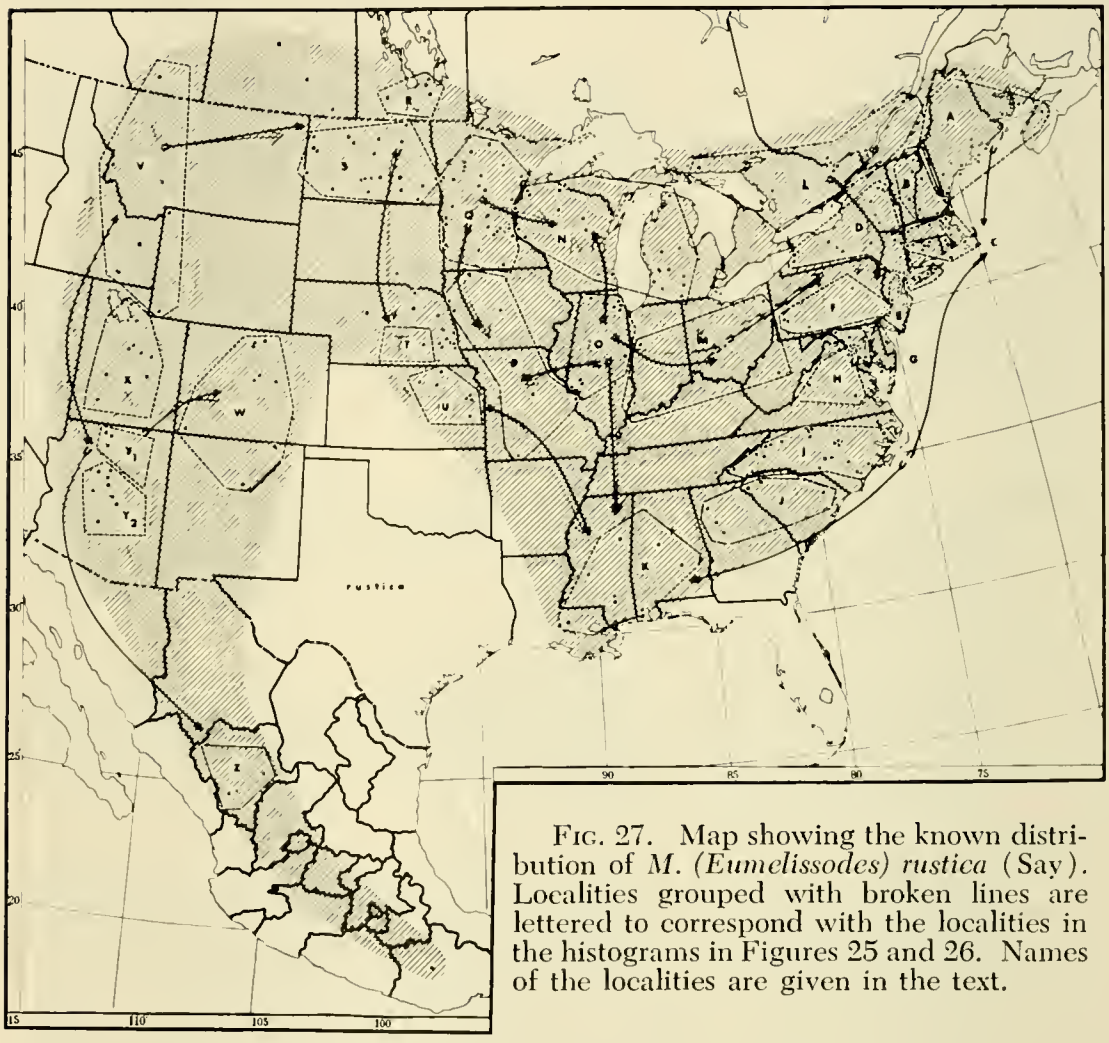


FIG. 27. Map showing the known distribution of *M. (Eumelissodes) rustica* (Say). Localities grouped with broken lines are lettered to correspond with the localities in the histograms in Figures 25 and 26. Names of the localities are given in the text.

Generally, the graphs show that the females are palest in the west and become progressively paler eastward. This is in accordance with the general rule of variation in the genus *Melissodes* (and related genera) previously proposed by LaBerge (1956, p. 917). However, the cline from west to east is not even, but various populations show deviations from the expected color pattern and several sublines occur in directions other than west-east. For instance, among the easternmost tier of populations the palest is from

North Carolina (I). Populations to the north of this region are progressively darker and the darkest are the southern New England populations (C). To the south of North Carolina the populations again become progressively darker and the darkest are the Alabama, Mississippi, Louisiana populations (K), although there are so few specimens from the latter areas that this conclusion is tentative.

Females from Illinois (O) are paler than those from areas to the north (N), the east (M), or the south (K). This is probably due to gene flow from western populations entering Illinois via the eastern extension of the prairies which reaches into that state. The palest of the prairie populations are in the northernmost part of the range and the populations in eastern Nebraska (T), eastern Kansas (U), and southeastward through Missouri become progressively darker. Specimens are lacking from the western parts of the great plains, except in the north (North Dakota, Manitoba, and Saskatchewan), and the species may well be absent from this area.

In the western parts of the species range, all females are quite pale in color. The palest population occurs in northern Arizona (Y1) and to the north and northeastward from this area the populations are slightly darker. Also, populations to the south (Central Arizona -Y2, Durango -Z) of this area are again somewhat darker in color.

This complicated system of minor clines within the major east-west cline is represented on the distribution map (Fig. 27) by a system of arrows. The palest populations are at or near the bases and the darker populations at or near the heads of the arrows. It should be emphasized that in several cases the lack of sufficiently large samples makes this description of the distribution of melanism quite tentative. In some cases females were grouped where they, perhaps, should not have been, simply because there were too few specimens from certain areas. For instance, specimens from Iowa were grouped with those from Missouri (P). Those from Iowa are very pale and intermediate between those from Nebraska and those in Illinois. The females from Missouri, on the other hand, are dark and are intermediate between the eastern Kansas females and the gulf coast populations. In all such cases, these facts were taken into account before drawing the arrows indicating subclines. In addition, specimens are almost wholly lacking from some areas of interest, such as Kentucky and Tennessee.

It should be evident from the facts of distribution presented here that each population is characterized by its own peculiar combination of characters (Fig. 25). Furthermore, the clines and subclines

do not exhibit any clear steps or breaks which one could logically use as limits for subspecies. A western and an eastern race might be recognized subspecifically, but this would result in a very large, rather indeterminate, intervening area in which the populations are intermediate in average melanism. In addition the populations in eastern Nebraska and eastern Kansas (and probably Iowa) would geographically fit into the eastern race or subspecies, but morphologically they are closer to the western race from which they are separated by a gap in the western parts of Nebraska and Kansas. Such a situation would not be taxonomically suitable and would make curating of specimens more difficult (because of the large number of intermediate specimens), rather than simplified.

In addition to color variation, the western populations average slightly larger than the eastern populations. But this character is not distributed in a generally east-west cline in the same fashion as is color. Time has not permitted the study of size variation in *M. rustica* at present.

Bionomics. This species is oligolectic on Compositae, as are most species of *Eumelissodes.* In the eastern parts of its range, it seems to prefer species of the genera *Solidago* and *Aster.* In the western parts of the range, it seems to prefer *Solidago, Aster, Grindelia* and *Aplopappus* in approximately that order. The flower data available from labels on specimens are summarized in Table XIV.

Type Material. Type specimens of *rustica* Say are destroyed. Lectotype, here designated, female of *simillima* Robertson collected by Charles Robertson at Carlinville, Illinois, September 15, 1889, on *Helenium autumnale* (Coll. No. 3259), and the lectoallotype male, here designated, of *simillima* Robertson collected by Charles Robertson at Carlinville on August 21, 1896, on *Helianthus divaricatus* (Coll. No. 18071) are in the collection of the Illinois Natural History Survey at Urbana. The holotype female of *ambigua* Smith from Mexico is in the British Museum (Natural History) in London (Type No. 17-B-837). The holotype female of *assimilis* Smith from Oaxaca, Mexico, in the British Museum (Natural History) (Type No. 17-B-862). The holotype female of *festinata* Provancher is in the Provancher collection in the Provincial Museum, Quebec, Canada. The lectotype female, here designated, of *asteris* Robertson, collected by Charles Robertson at Carlinville, Illinois, September 29, 1902, on *Aster ericoides villosus* is in the collection of the Illinois Natural History Survey at Urbana.

Distribution. *M. rustica* ranges from Nova Scotia in the northeast to Saskatchewan in the west and south to Georgia, Louisiana, New Mexico and Durango (Fig. 27). This species has been collected from May 31 to November 23, but chiefly during August and September. In addition to the type material, 904 females and 774 males

TABLE XIV. Summary of Floral Records for *Melissodes rustica.*

Plant Data			Records of *M. rustica*			
FAMILY	Number of genera	Approximate number of species	Number of collections	Number of females	Number of males	Total number of bees
Compositae:						
Solidago spp.	1	8	58	73	57	130
Aster spp.	1	9	48	95	14	109
Grindelia spp.	1	1	26	25	26	51
Aplopappus spp.	1	1	6	26	2	28
Helianthus spp.	1	3	11	7	7	14
Chrysopsis spp.	1	1	3	13	1	14
Other genera	13	13	22	12	29	41
Brassicaceae	1	2	3	7	3	10
Labiatae	4	4	4	3	7	10
Leguminosae	1	2	3	2	3	5
Other families (3)	4	4	5	0	8	8
Totals	29	48	189	263	157	420

have been examined from the localities listed below. Localities reported in the literature are included in this list.

ALABAMA: Boothton; Kushla; Montgomery. ARIZONA: Flagstaff; Grand Canyon; Houserock Valley; Jacobs Lake (6 miles N.), Coconino Co.; Oak Creek Canyon; Payson; Phoenix; Pine (2.9 miles N.); Prescott; Sedona; Williams. COLORADO: Bailey; Crossons; Elbert; Estes Park; Fort Collins; Glen Haven; Mesa Verde; Stonewall. CONNECTICUT: Colebrook; East Hartford; Manchester; Canaan; Rockville, Stafford; Storrs. DELAWARE: "Del." DISTRICT OF COLUM-

BIA: Anacostia, Carberry Meadow; Potomac Flats; Washington. GEORGIA: Atlanta; Cartersville; Griffin; Thomsons Mills. IDAHO: Idaho Falls; Roy. ILLINOIS: Berwin; Carlinville; Chicago; Elsah (Principia College); Fairmount; Macoupin Co.; Olive Branch; Palos Park; Rockford; Wilmette. INDIANA: Gibson Co.; Lafayette; Rush Branch. IOWA: Ames; Dickinson Co.; Onawa; Sioux City. KANSAS: Baldwin; Cloud Co.; Garnett; Lawrence; Lone Star Lake, Douglas Co.; Marysville; Riley Co. LOUISIANA: Addis. MAINE: Casco; Eliot; Indiantown Island; Leeds; Little Deer Island; Mt. Desert Island; Orono; Saco; Squirrel Island; Waldoboro; Washburn. MARYLAND: Beltsville; Bethesda; Cabin John; Chesapeake Beach; College Park; Glen Echo; Hancock; Mt. Airy; Plummers Island; Yarrow. MASSACHUSETTS: Dedham; Duxbury; Forest Hills; Framingham; Hinsdale; Holden; Holliston; Middlesex Falls; Nantucket; Natick; Needham; North Attleboro; Reading Highlands; Wellesley; Woods Hole. MICHIGAN: Allegan Co.; Cheboygan (12 miles S. W.); Douglas Lake; Grand Rapids; Hillsdale Co.; Ingham Co.; Ionia Co.; Ironwood; Jackson Co.; Kalamazoo Co.; Keweenaw Co.; Mecosta Co.; Midland Co.; Muskegon Co.; Oceana Co. MINNESOTA: Barrett; Beltrami Co.; Bengal; Bigstone Co.; Carver Co. (Zumbro Heights); Cass Co.; Clay Co.; Cokato; Detroit Lakes; Duluth; Fort Snelling; Hastings; Hayward; Hendricks; Hennepin Co.; Itasca State Park; Koochiching Co.; Lake Itasca; Lake Lena; Lake Vadnais; Ramsey Co.; Minnetonka Lake; Moorhead; Ortonville; Pelican Lake; Pine Co.; Pine River; Ramsey Co.; Savannanoa; Shevlin; Sleepy Eye; St. Anthony Park; St. Cloud; St. Paul. MISSISSIPPI: Camp Shelby; Hattiesburg; Jackson; State College. MISSOURI: Branson; Columbia; St. Louis. MONTANA: Hamilton; Three Forks. NEBRASKA: Ashland; Cedar Bluffs; Halsey; Lincoln; Malcolm; Nebraska City; Neligh; Niobrara; Omaha; Wabash; Weeping Water; West Point, York Co. NEW HAMPSHIRE: Alstead; Durham; Franconia; Lancaster; Pelham. NEW JERSEY: Englewood; Fort Lee; Gloucester; Lakewood; Montclair; Newark; New Brunswick; Palisades Park; Plainfield; Pt. Pleasant; Ramsey; South Orange; Trenton; Westville. NEW MEXICO: Chicoric Canyon (near Raton); Rowe. NEW YORK: Brooklyn; Cold Spring Harbor; Copake Falls; Covert; Seneca Co.; East Aurora; Geneva; Gloversville; Gowanda; Hague; Hamburg; Ithaca; Keene Valley, Essex Co.; Lake Placid; Long Island (sea cliffs); Long Lake (7 miles S.); Moshalu; New Baltimore; New Rochelle; New York City; Nyack; Oneonta; Pine Island; Poughkeepsie; Quogue; Southampton; Speculator; Staten Island; Tappan;

Tuxedo Park. North Carolina: Black Mountains (valley of); Bryson City; Busick; Burgaw; Church Island; Crabtree Creek St. Park; Davidsons River; Doughton Point; Grandfather Mt.; Holly Shelter; Lakeview; Linville; McCullers; Marion; Mayodan; Rockingham Co.; Moyoc; New River; Raleigh; Reidsville; Richmond Co.; Sampson Co.; Spout Springs; Wake Co.; Washington Co.; Wilkesboro. North Dakota: Beach; Bismarck; Cannon Ball; Carpio; Devils Lake; Edgeley; Enderlin; Fargo; Jamestown; McKenzie; Mandan; Martin; Minot; Mott; Nicholson; Rawson; Rugby; Schafer; Steele; Wales; Williston. Ohio: Columbus; Trumbull Co. Pennsylvania: Bloomsburg; Braddock; Central City, Darby; Delaware Co.; Glenside; Lawndale; Philadelphia; Pittsburgh; Wilawana. Rhode Island: Block Island; Providence. South Carolina: Clemson College; Florence; Greenville. South Dakota: Platt. Tennessee: Monroe Co. Utah: Alta (2 miles W.); Carbon Co.; Clear Creek Canyon; Cove Fort; Emery Co.; Lakepoint; Mt. Nebo; Ogden; Parowan; Pine Valley Mts.; Thistle Canyon. Vermont: Lyndon; Woodstock. Virginia: Alexandria; Barcroft; Falls Church; Fort Humphreys; Glencarlyn; Goshen; Kearney; Long Bridge (S. end of); Loudoun; Newington; Richmond; Rosemont; Tangier Island. West Virginia: Millville; Southburg. Wisconsin: Farmington; Hudson; Iron Co.; Langlade Co.; Maiden Rock; Milwaukee; Morris; Price Co.; Randall; St. Croix Dam, Douglas Co.; Wascott. Wyoming: Uinta Co.; Yellowstone National Park. *Canada.* Alberta: Lethbridge. Manitoba: Aweme; Balmoral; Teulon; Treesbank; Winnipeg. New Brunswick: Nerepia, St. John. Nova Scotia: Kings Co. Ontario: Carp (5 miles W.); Muskoka; Ottawa; Spencesville; Sudbury; Toronto. Quebec: Aylmer (Queen's Park); Cap Rouge; Hemmingford; Hull; Kazabazua; Montreal. Saskatchewan: Earl Grey; Estevan; Saskatoon. *México.* Durango: Coyotes El Salto (6 miles N. E.); Otinapa; Palo Colorados. Oaxaca: Oaxaca.

Flower Records. Abutilon theophrasti, Amphiachyris dracunculoides, Aplopappus sp., *A. gracilis, Asclepias* sp., *Aster* sp., *A. anomalus, A. commutatus, A. crenulis, A. dumosus, A. ericoides, A. e. villosus, A. exiguus, A. grandiflorus, A. laevis, A. lateriflorus, A. multiflorus, A. novaeangliae, A. paniculatus, A. praeatus, A. sagittifolius, A. salicifolius, A. turbinellus, Baccharis* sp., *Bidens aristosa, B. laevis, B. asteroides, Centaurea juncea, Chrysopsis* sp., *C. mariana, Cirsium arvense, C. lanceolatum, Cleome lutea, C. serrulata, Coreopsis tripteris, Cosmos* sp., *Epilobium* sp., *E. perfoliatum, Gail-*

lardia sp., *Grindelia* sp., *G. squarrosa, Helenium* sp., *H. autumnale, H. tenuifolium, Helianthus* sp., *H. atrorubens, H. divaricatus, H. grosse-serratus, H. maximillianus, H. petiolaris, H. radula, H. tuberosus, Heliopsis helianthoides, Hieracium scabrum, Lycopus americanus, Marrubium vulgare, Melilotus alba, M. officinalis, Mentha* sp., *Physostegia parviflora, Polymentha* sp., *Ratibida columnaris, R. pinnata, Rudbeckia laciniata, R. subtomentosa, R. triloba, Silphium perfoliatum, Solidago* sp., *S. altissima, S. canadensis, S. graminifolia, S. juncea, S. nemoralis, S. rigida, S. rugosa, S. serotina, Spiraea alba, Verbena* sp., *V. hastata, V. stricta, Verbesina virginica, Vernonia fasciculata, V. glauca.*

Melissodes (Eumelissodes) grindeliae Cockerell

Melissodes grindeliae Cockerell, 1898, Bull. Sci. Labs. Denison Univ., vol. 11, pp. 66, 67; 1899, Bull. Univ. New Mexico, vol. 1, pp. 66, 67; 1899, Canadian Ent., vol. 31, p. 256; 1901, Ann. Mag. Nat. Hist., ser. 7, vol. 7, p. 130; 1901, Ent. News, vol. 12, p. 40; 1903, Ann. Mag. Nat. Hist., ser. 7, vol. 12, p. 450; 1905, Bull. S. California Acad. Sci., vol. 4, p. 103; 1906, Trans. Amer. Ent. Soc., vol. 32, pp. 77, 88, 92; 1906, Trans. Amer. Ent. Soc., vol. 32, p. 309; Viereck, 1906, Trans. Amer. Ent. Soc., vol. 32, p. 238; Snow, 1906, Trans. Kansas Acad. Sci., vol. 20, p. 237; Cockerell, 1907, Univ. Colorado Studies, vol. 4, p. 255; Tucker, 1909, Trans. Kansas Acad. Sci., vol. 22, p. 281; Cockerell, 1910, Ann. Mag. Nat. Hist., ser. 8, vol. 5, p. 257; 1919, Jour. New York Ent. Soc., vol. 27, p. 300; 1930, Amer. Mus. Nov. No. 397, p. 1; Brimley, 1938, Insects of North Carolina, p. 462.

This species is related to *M. rustica* and *M. pallidisignata,* but can be distinguished from these species by the longer first flagellar segments of the male, the broader pale pubescent bands of the terga, and the sparser and finer punctation of the terga of both sexes as described below. In addition, the female differs from those of *rustica* and *pallidisignata* by the generally ochraceous scopal hairs, ochraceous to yellow pale pubescent tergal bands (especially on terga 3 and 4), and the presence of fine, suberect hairs in the apical areas of terga 2 and 3.

Female. Measurements and ratios: N, 20; length, 10-13 mm.; width, 3.0-4.5 mm.; wing length, $M = 3.82 \pm 0.178$ mm.; hooks in hamulus, $M = 12.70 \pm 0.193$; flagellar segment 1/segment 2, $M = 1.98 \pm 0.027$.

Structure and color: Integument black except as follows: apical half of mandible and distitarsi rufescent; flagellar segments 3-10 slightly rufescent beneath, especially last 3 or 4 segments; eyes blue to grayish green; wing membranes slightly infumate, veins brown to black; tegulae piceous; tibial spurs white to slightly rufescent; metasomal tergum 1 with extremely narrow apical margin hyaline.

Structure and punctation as in *pallidisignata* except as follows:

clypeal punctures large, shallow, round, separated mostly by half a puncture width except medially where longitudinal median carina usually present at least in apical half; galeae above shiny, unshagreened except at extreme tips; maxillary palpal segments in ratio of about 4.0:2.5:2.5:1.0, first and last segments often shorter. Mesoscutum with anterior third punctures deep, separated by one-third to one puncture width (but mostly by less than one), posteromedian area punctures separated mostly by two to four puncture widths; surface often slightly dulled by extremely fine, reticular shagreening; mesepisternal punctures distinct, separated by half a puncture width or less, surface shiny, unshagreened or slightly so. Tergum 1 with basal three-fifths with punctures small, shallow, separated by two to three puncture widths (medial half), apical area impunctate, surface dulled by fine, dense, reticulotranverse shagreening, apical and basal areas not strongly contrasting in shagreening; tergum 2 with basal area punctures minute, distinct, separated by two to three puncture widths, interband zone punctures of similar size or smaller, extremely sparse and often absent medially, apical area impunctate, surface of basal area shiny to slightly dulled, of interband and apical area dulled by shagreening as in tergum 1; terga 3 and 4 similar to 2 but basal punctures more abundant and apical areas smaller or absent; terga 2 and 3 without conspicuously larger punctures at bases of bristlelike hairs.

Hair: Head white to pale ochraceous with abundant dark brown on vertex; thorax laterally white to pale ochraceous, occasionally mesepisterna brown on ventral, anterior and lower lateral surfaces, dorsally scutellum dark brown except pale fringe and mesoscutum with posteromedian dark patch extending forwards usually beyond a transverse line at anterior margins of tegulae, pale hairs of mesoscutum pale ochraceous to yellowish, but not rufescent. Tergum 1 with basal area ochraceous to yellowish; tergum 2 with basal area white to pale ochraceous, interband zone dark brown, distal band pale ochraceous to slightly yellow, basal and distal pale bands connected at extreme sides by pale pubescence, distal band not usually interrupted medially, but narrowed and often reaching apex at extreme sides, apical area with abundant, suberect, ochraceous to brown, relatively simple, long hairs (unless worn); tergum 3 similar except basal tomentum dark brown, distal band broader, reaching apex of tergum in about lateral thirds, often slightly yellowish, tergum 4 with apical pale band usually yellowish to almost orange, of equal width across tergum, never interrupted;

terga 5 and 6 with small tufts of pale hairs laterally; sterna dark brown, usually pale laterally. Legs white to ochraceous except as follows: anterior tarsi, middle and hind distitarsi, inner surfaces middle and hind basitarsi, and pygidial plates reddish brown to dark brown.

Male. Measurements and ratios: N, 20; length, 9-12 mm.; width, 2.5-4.0 mm.; wing length, $M = 3.56 \pm 0.166$ mm.; hooks in hamulus, $M = 12.05 \pm 0.235$; flagellar segment 2/segment 1, $M = 3.22 \pm 0.062$.

Structure and color: Integument black except as follows: clypeus yellow except rufescent to piceous apical margin; apical half of mandible and distitarsi rufescent; eyes green to yellow-brown; wing membranes colorless to slightly infumate, veins reddish brown to dark brown; tegulae piceous; tibial spurs yellow to rufescent; apical areas of terga hyaline, colorless to yellow; labrum and mandibles without yellow spots.

Structure as in *pallidisignata* except as follows: first flagellar segment minimum length about one-third maximum length of second segment, penultimate segment three times as long as broad or shorter, flagellum just reaching pterostigma in repose or shorter; maxillary palpal segments in ratio of about 3.0:2.0:2.2:1.0, last segment often shorter, second segment often slightly longer. Sculpturing as in female except as follows: mesoscutal posteromedian impunctate area often smaller or with sparse punctures; tergum 1 with basal four-fifths to five-sixths punctate, punctures slightly larger, separated by one to three puncture widths; tergum 2 with basal area punctures separated by one to three puncture widths; terga 2-4 with interband zone punctures slightly coarser and slightly more abundant; sterna usually with surface somewhat dulled by reticular shagreening. Terminalia as in *rustica.*

Hair: Head and thorax with pale hairs white to yellow, brighter on dorsum of thorax, vertex often dark brown, scutellum and mesoscutum usually with abundant dark brown, most often lacking on mesoscutum, tegulae usually with at least a few brown hairs. Tergum 1 ochraceous; tergum 2 as in female but interband zone hairs erect and partly pale, apical area hairs suberect, longer and often brown; terga 3 and 4 similar to 2 but interband zone erect hairs partly to wholly brown, distal pale pubescent bands reaching apex of tergum at least in lateral thirds, on tergum 4 often across entire tergum; tergum 5 similar to 4 but apical area obliterated; terga 6 and 7 yellow apically, brown basally; sterna yellow to brown

TABLE XV. Summary of Floral Records for *Melissodes grindeliae*.

Plant Data			Records of *M. grindeliae*			
FAMILY	Number of genera	Approximate number of species	Number of collections	Number of females	Number of males	Total number of bees
Compositae:						
Ratibida spp.	1	2	5	54	8	62
Chrysopsis sp.	1	1	2	76	10	86
Rudbeckia sp.	1	1	1	19	0	19
Haplopappus sp.	1	1	1	10	0	10
Grindelia sp.	1	1	4	7	0	7
Others	7	7	10	8	42	50
Leguminosae	3	5	7	2	8	10
Other families	5	5	6	5	22	27
Totals	20	23	36	181	90	271

medially. Legs pale ochraceous to yellow except golden yellow to orange on inner surfaces of tarsi.

Bionomics. *M. grindeliae* is an oligolege of composites, but it is not restricted to the genus *Grindelia* for pollen, as its name implies. In fact, *Grindelia* seems to play a relatively small role in the flower preferences of this bee. Table XV summarizes the floral data available from labels on specimens examined by the author. It can be seen that several genera of composites other than *Grindelia* are as important, if not more so, than the latter as pollen sources for this bee.

Type Material. Cockerell (1898) apparently did not select a holotype from among the specimens from which he described this species. I have seen three specimens which are undoubtedly a part of the original type series, although none of them are marked as types. Of these I hereby select as the lectotype of *grindeliae* a female bearing the following collection data: Ckll. 3943; Sta. Fe; July; on *Lepachys*. This specimen bears a label in Cockerell's hand identifying the bee as *Melissodes grindeliae*. This specimen is in

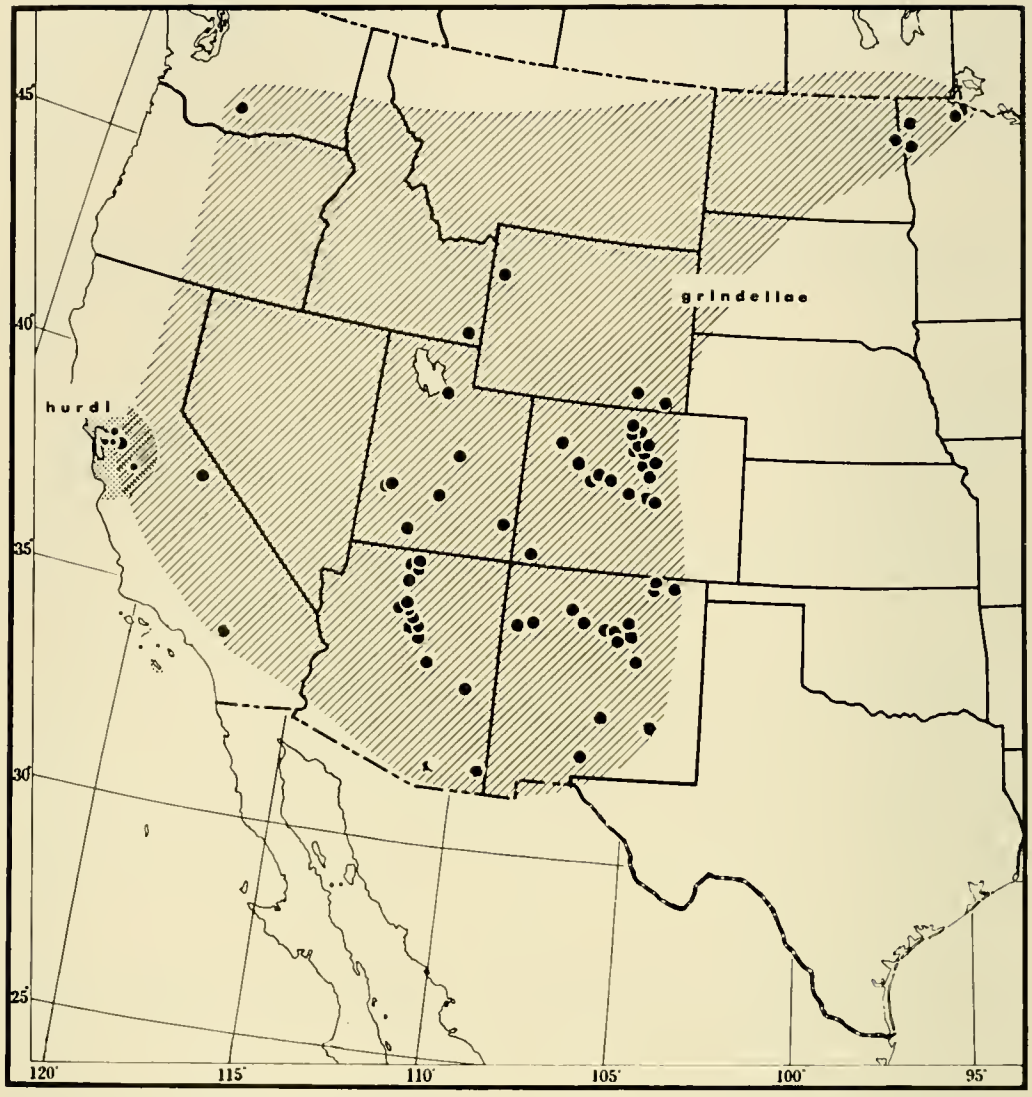


FIG. 28. Map showing the known distributions of *M. (Eumelissodes) grindeliae* Cockerell and *M. (E.) hurdi* LaBerge.

the collection of P. H. Timberlake at the Citrus Experiment Station, Riverside, California.

Distribution. This species is distributed from Washington and Idaho to Arizona and New Mexico and from California to Minnesota and Colorado (Fig. 28). It has been collected from June 26 to September 27, but mainly during July. Including the type material, 367 females and 188 males have been examined from the localities listed below (the list includes records from the literature).

ARIZONA: Chiricahua Mts. (Rustlers Camp), Cochise Co.; Coconino Co.; Flagstaff; Grand Canyon; Houserock Valley; Humphreys Peak (at base); Jacob Lake (11 miles N. W.); Kaibab Forest; McNary Junction (6 miles S.), Apache Co.; Maine, Coconino Co.; Mogollon Rim; Mormon Lake; Oak Creek Canyon; San Francisco

Mts.; Santa Rita Mts.; Todd's Lodge, Oak Creek Canyon; Walnut Canyon (near Flagstaff). California: Antioch; Mammoth; Upper Santa Ana River, San Bernardino Co. Colorado: Aspen; Aurora (Bear Creek); Big Thompson Canyon; Boulder; Colorado Springs (Palmer Park); Eleven-mile Canyon, Park Co.; Estes Park; Glen Haven; Glenwood Springs; Golden (Lookout Mt.); Jim Creek (near Boulder); La Poudre River (Indian Meadows); Leadville; Meeker; Mesa Verde; Mt. Alto; Overland Lake, Boulder Co.; Peaceful Valley; Platte Canyon; Rock Creek Canyon (near Colorado Springs); Sedalia. Idaho: Cub River Canyon. Minnesota: Baudette; Lake of the Woods Co.; Marshall Co.; Polk Co. New Mexico: Capulin; Colfax Co.; Dripping Spring (Organ Mts.); Jemez Springs; La Jara (5 miles E.), Sandoval Co.; La Tenaja; Las Vegas; Nogal; Pecos; Raton Pass; Roswell (5 miles S.); Rowe; Sandia Mts.; San Ignacio; Santa Fe; Sapello; Thoreau (8 miles N.), McKinley Co.; Tuerto Mts. North Dakota: Grand Forks; Hardeys Peak. Utah: Alton; Beaver Mts.; Beaver Valley; Bicknell (17 miles S.); Cedar Point; Clear Creek Canyon; Lake Canyon; Monticello; Salt Lake. Washington: White Swan (8 miles S. W.), Yakima Co. Wyoming: Cheyenne; Grand Teton National Park; Laramie.

Flower Records: Aster commutatus, Chrysopsis hispida, Chrysothamnus nauseosus, Cleome sp., *C. serrulata, Croton* sp., *Grindelia* sp., *G. squarrosa, Haplopappus* sp., *Helianthus* sp., *Hymenoxys floribunda, H. richardsonii, Liatris punctata, Lupinus* sp., *Melilotus* sp., *M. alba, M. officinalis, Petalostemum* sp., *P. occidentale, Phacelia glandulosa, Polymentha* sp., *Psilostrophe gnaphaloides, Ratibida* sp., *R. columnaris, R. tagetes, Rudbeckia laciniata, Verbena stricta.*

Melissodes (Eumelissodes) hymenoxidis Cockerell

Melissodes hymenoxidis Cockerell, 1906, Bull. Amer. Mus. Nat. Hist., vol. 22, p. 443; 1910, Psyche, vol. 17, p. 246; 1915, Ann. Mag. Nat. Hist., ser. 8, vol. 15, p. 269; 1918, Ann. Mag. Nat. Hist., ser. 9, vol. 1, p. 160; 1928, Univ. Colorado Studies, vol. 16, p. 114; 1933, Trans. Ent. Soc. Amer., vol. 26, p. 44; 1936, Amer. Mus. Nov. No. 831, p. 5; Bohart, Knowlton and Bailey, 1950, Utah St. Agric. Col., Mimeo. Ser. 371, p. 5.

Melissodes fremontii Cockerell, 1907, Entomologist, vol. 40, p. 268 (new synonymy); Clements and Long, 1923, Expt. Pollination, Carnegie Inst. of Washington, Publ. No. 336, p. 249.

Melissodes kelloggi Cockerell, 1919, Ent. News, vol. 30, p. 293 (new synonymy); 1928, Univ. Colorado Studies, vol. 16, p. 114; Bohart, Knowlton and Bailey, 1950, Utah St. Agric. Col., Mimeo. Ser. 371, p. 5.

Melissodes hymenoxidis is a small dark bee related to *M. rustica* and *M. grindeliae.* Both sexes are distinctive in the extremely shiny surfaces of the body, especially of the terga. The second tergum has the interband zone completely without shagreening in the lat-

eral raised areas (shagreening is not visible here even at magnifications of 100 times with a dissecting scope). The female has abundant dark hair on the head, lateral surfaces of the thorax and abdomen, much as in the darker specimens of *rustica,* but the pale hairs of the head and thorax are white or cinereous rather than ochraceous to rufescent. The males have the long second flagellar segments of this group of species and hyaline tergal apices.

Female. Measurements and ratios: N, 20; length, 10-12 mm.; width, 3-4 mm,; wing length, $M = 3.45 \pm 0.128$ mm.; hooks in hamulus, $M = 11.90 \pm 0.261$; flagellar segment 1/segment 2, $M = 2.07 \pm 0.035$.

Structure and color: Integument black except as follows: apical half of mandibles and distitarsi rufescent; eyes green; flagellar segments 3-10 dark reddish brown below; tibial spurs yellow; wing membranes hyaline, veins dark brown; tegulae piceous; apical margin of tergum 1 narrowly hyaline or lighter brown.

Structure and sculpture as in *pallidisignata* except as follows: clypeus usually with well-marked median longitudinal carina; clypeus and supraclypeal area with surface unshagreened, shiny; galeae unshagreened above, or slightly so in apical half or less; vertex with flattened lateral areas with small punctures, surface unshagreened; mesoscutal punctures small and crowded anteriorly (here smaller than mesepisternal punctures), posteromedially sparse or absent, surface unshagreened; mesepisternal punctures size of posteromedian mesoscutal punctures, separated mostly by half a puncture width or less, surface unshagreened; tergum 1 with basal three-fifths punctate, punctures shallow, large, separated mostly by half to one puncture width (medially), or slightly more, surface somewhat dulled by fine reticular shagreening, apical impunctate area with extremely fine reticulotransverse shagreening scarcely dulling surface; tergum 2 with basal area punctures separated mostly by half a puncture width, surface unshagreened, interband zone punctures large, deep, separated by one to three puncture widths, surface shiny, extremely finely shagreened medially and completely unshagreened in lateral raised areas, apical area as in tergum 1; tergum 3 similar to 2 but interband zone punctures slightly more crowded and apical area smaller and with minute round punctures near distal pubescent band; tergum 4 with apical area lacking.

Hair: Pubescence and hair long, slender, shiny and silky (especially on abdomen). Head black except a few cinereous hairs on face below vertex. Thorax with sides black to dark brown; above

white to cinereous except medial scutellar hairs and small postero-median mesoscutal patch of brown; tegulae usually with some brown; dorsal and posterior surfaces of propodeum white to cinereous. Tergum 1 dark brown on anterior and lateral surfaces, dorsally white to cinereous except brown posterolaterally; tergum 2 with basal tomentum white, interband zone with erect to suberect, dark brown hairs and many strong and bristlelike, distal pubescent band dark brown or pale in lateral fourth of tergal width, distal band when pale not connected with pale basal tomentum nor reaching apex of tergum laterally; tergum 3 similar to 2 but basal tomentum dark brown, distal pubescent band white, although usually interrupted medially and often by as much as one-third tergal width, apical area with abundant subappressed, relatively simple, long, dark brown hairs; tergum 4 with apical pale band narrower than basal dark area and usually interrupted medially by brown but not so much as in tergum 3; tergum 5 and 6 and sterna dark brown to black. Legs brown to dark brown except as follows: scopal hairs pale ochraceous to yellow except apically on basitarsus and on basitibial plates, hind tibiae on inner surfaces yellow.

Male. Measurements and ratios: N, 14; length, 9-11 mm.; width, 2.5-3.0 mm.; wing length, M = 3.09 ± 0.095 mm.; hooks in hamulus, M = 10.93 ± 0.287; flagellar segment 2/segment 1, M = 3.48 ± 0.376.

Structure and color: Integument black except as follows: apical half of mandibles, distitarsi and often basitarsi and tibiae rufescent; clypeus yellow except reddish brown apical margin; labrum and mandibles without pale maculae; flagellum yellow beneath, dark reddish brown to black above (segment 2 often entirely brown); eyes bluish green to green; wing membranes colorless, veins reddish brown to black; tegulae piceous; tibial spurs yellow; tergal apical areas hyaline, colorless.

Structure as in *pallidisignata* except as follows: flagellum reaching prestigma and rarely pterostigma in repose; maxillary palpal segments in ratio of about 7:7:4:1, second segment often slightly less and last segment as much as twice as long. Sculpturing as in female except as follows: tergum 1 with basal five-sixths or more punctate; tergum 2 with basal zone punctures separated by about half a puncture width at extreme base to two or three puncture widths near interband zone, interband zone with surface extremely shiny and unshagreened even medially; terga 3-5 similar to tergum

2 but punctures more abundant in interband zones. Terminalia as in *rustica*.

Hair: Vestiture silky as in female; white to cinereous except as follows: vertex occasionally with sparse brown hairs; scutellum occasionally and mesoscutum rarely with brown medially; terga 2-5 with interband zones partly or wholly brown, bristlelike hairs abundant, strong, often dark, erect; terga 2-6 with complete white distal pubescent bands and terga 3-4 with a few subappressed, white relatively simple, apical hairs; terga 3-5 with basal tomentum brown; terga 6 and 7 pale; sterna pale or slightly yellowed medially; legs white except inner surfaces of tarsi yellow.

Bionomics. Little can be said about the flower preferences of *hymenoxidis*, since the floral records are too sparse. It has been collected on a mint (one female), on *Grindelia* (one female), and (type series) two females were seen to visit successively *Hymenoxys ligulaeflora* and *Chrysopsis* sp.

Type Material. Cockerell described *M. hymenoxidis* from a series of three females. Of these, two have been located and both bear the label "cotype." The third specimen, which was presumably the holotype, has been lost or destroyed. As Cockerell did not refer to any single specimen in his original description as the holotype, the lost specimen cannot be certainly identified as such. Therefore, the female specimen in the collection of the American Museum of Natural History, New York City, is hereby designated as the lectotype of *M. hymenoxidis* Cockerell (AMNH Type No. 21149). This female was taken by T. D. A. Cockerell at Florissant, Colorado on July 17. The holotype male of *kelloggi*, collected by T. D. A. Cockerell at Longs Peak Inn, Colorado on July 19, is in the collection of the U. S. National Museum (Type No. 22591). The holotype male of *fremontii*, collected by S. A. Rohwer at Florissant, Colorado on July 23, 1907, is in the collection of the Museum of Natural History at the University of Colorado, Boulder.

Distribution. *M. hymenoxidis* ranges from eastern California to Colorado and north to Montana (Fig. 15). It has been collected from June 25 to August 29, but mainly in July. In addition to the type material, 47 females and 15 males have been examined from the localities listed below (this list includes records reported in the literature).

CALIFORNIA: Convict Lake, Mono Co.; Duck Lake, Mono Co.; Walker River (Leavitt Meadow), Mono Co. COLORADO: Boulder Co. (Science Lodge); Creede; Eldora; Florissant; Leadville; Longs

Peak Inn; Medicine Bow Mts.; Meeker; Ouray (Summit Road); Pingree Park, Larimer Co.; Tennessee Pass; Tolland; Ward. MONTANA: Missoula. UTAH: Randolph; Strawberry Reservoir. WYOMING: Bondurant; Grand Teton National Park; Owl Creek Mts.; Larimer (S. E.).

Flower Records. *Chrysopsis* sp., *Grindelia* sp., *Hymenoxys lingulaeflora*, a mint.

Melissodes (Eumelissodes) illata Lovell and Cockerell

Melissodes illata Lovell and Cockerell, 1906, Psyche, vol. 13, p. 110; Criddle, Curran, Viereck, and Buckell, 1924, Rept. Ent. Soc. Ontario, vol. 33, p. 99; Proctor, 1938, Biol. Surv. Mt. Desert Region, vol. 6, p. 444.

Melissodes illata is a small, dark, northern species from eastern North America. It is distinctive in the almost complete lack of punctation in the interband and apical areas of the terga of both sexes and differs in this way from members of the *coreopsis* group to which it appears to be allied. It is closely related to the species immediately following and the differences are given in the diagnosis of the latter.

Female. Measurements and ratios: N, 20; length, 8-11 mm.; width, 3-4 mm.; wing length, M = 3.08 ± 0.113 mm.; hooks in hamulus, M = 11.35 ± 0.196; flagellar segment 1/segment 2, M = 1.88 ± 0.033.

Structure and color: Integument black except as follows: apical half of mandible and distitarsi rufescent; flagellar segments 3-10 paler beneath but rarely red, usually dark brown, often mostly black; eyes dark gray to green; wing membranes clear, slightly infumate, veins black; tegulae piceous; tibial spurs yellow; tergum 1 with apex extremely narrowly or not at all hyaline.

Clypeus flat as in *coreopsis*, with crowded punctures separated mostly by half a puncture width or slightly more, dulled by coarse reticular shagreening; supraclypeal area with sparse punctures, almost always opaque, dulled by coarse tessellation; galeae above shiny, usually unshagreened or with shagreening in less than apical half, rarely more; lateral areas of vertex with small punctures separated mostly by two to four puncture widths, surface shiny; maxillary palpal ratio about 2.8:2.4:2.0:1.0, occasionally with minute fifth segment present. Mesoscutum with deep round punctures anteriorly and peripherally separated by half to one and posteromedially by one to three puncture widths, surface often with fine tessellation especially posteromedially; scutellum similar to mesoscutum; mesepisternum with punctures larger and shallower than

mesoscutal, surface dulled by irregularly reticulate shagreening or fine tessellation at least in upper third. Metasomal tergum 1 with shallow punctures in basal three-fifths separated mostly by one puncture width, apical area impunctate, anterolateral lobes of apical area impunctate or punctures sparse, surface dulled by dense reticulotransverse shagreening especially basally; tergum 2 with basal area punctures minute, separated mostly by two puncture widths or more, surface shiny or dulled by reticular shagreening, with interband zone impunctate or with sparse, irregular punctures peripherally, surface as basal area of tergum 1, with apical area impunctate, surface dulled as in tergum 1; tergum 3 similar to 2; tergum 4 similar but beneath apical pubescence medially with minute punctures usually less than twice diameter of hairs arising from them; pygidial plate V-shaped, basal width subequal or slightly more than median length, apex rounded.

Hair: Pale hairs and pubescence white except extremely pale ochraceous on mesoscutum and pronotum; vestiture in general as in darker specimens of *coreopsis*. Head with abundant dark brown on vertex and often brown on labrum and apex of clypeus. Mesoscutum with posteromedial dark patch more than twice size of scutellar dark area, often mesoscutal hairs almost all black; posterior pronotal lobes usually with at least a few dark hairs and often most pronotal hairs dark; ventral mesepisternal hairs occasionally dark brown. Tergum 1 pale basally, apically usually glabrous or with short, simple, appressed, dark brown hairs basally and in anterolateral lobes; tergum 2 with basal area white, distal pale band white, narrowly to broadly interrupted medially, interband zone with short, suberect, dark brown hairs, apical area with scattered, short, appressed, brown hairs near white pubescence and glabrous apically; tergum 3 similar to 2 but basal tomentum brown, distal white band usually narrowly interrupted and occasionally not at all, and apical area hairs more abundant; tergum 4 as in 3 but distal white band apical and interrupted medially by triangular area of suberect brown pubescence; tergum 5 usually with small lateral pale tufts; tergum 6 without lateral pale tufts; sterna dark brown, usually pale laterally. Legs as in *coreopsis* but scopal hairs often yellow.

Male. Measurements and ratios: N, 20; length, 8-10 mm.; width, 2.5-3.5 mm.; wing length, $M = 2.97 \pm 0.190$ mm.; hooks in hamulus, $M = 10.40 \pm 0.134$; flagellar segment 2/segment 1, $M = 7.38 \pm 0.102$.

Structure and color: Integument black except as follows: clypeus yellow except testaceous apical margin and dark tentorial pits; labrum with cream-colored mediobasal macula; mandibles rarely with minute basal yellow maculae; flagellar segments 2-11 usually red beneath, often somewhat infuscated towards base and tip; eyes gray-brown to green; wing membranes clear, veins dark brown; tibial spurs yellow; tegulae piceous; metasomal terga with apical areas piceous.

Structure and color: Structure as in *coreopsis* with the following exceptions and additions: minimum length first flagellar segment usually equals one-eighth to one-ninth maximum length second segment and always less than one-seventh second; maxillary palpal ratio about 4.0:3.3:3.3:1.0, rarely with minute fifth segment. Sculpturing as in female except as follows: tergum 1 with minute sparse punctures to within one-sixth of apical margin; terga 4 and 5 like tergum 3. Terminalia as in *agilis* but sternum 8 with ventral tubercle lamelliform with rounded apex; sternum 7 with median plate with ventral hairs sparse.

Hair: As in *coreopsis* except as follows: head with abundant brown on vertex: mesoscutum often mostly dark brown, always with at least a few brown hairs posteromedially; tergum 1 white basally, with short, brown, suberect to erect hairs apically; tergum 2 with distal white band narrow, occasionally uninterrupted, interband zone hairs longer, suberect to erect, apical area hairs sparse, long, subappressed to suberect; terga 3-5 usually with completely distal white bands, that on 5 often interrupted medially; terga 6 and 7 and sterna dark brown. Legs white except inner surfaces tarsi yellow.

Bionomics. This species is an oligolege of composites and seems to prefer the genera *Solidago* and *Aster* in that order. The floral data are too sparse, however, to give a clear indication of preferences.

Type Material. Lectotype male, here designated, of *illata* from Waldoboro, Maine, collected by J. H. Lovell, August 13, 1905, on *Solidago* sp., is in the collection of T. B. Mitchell, North Carolina State College, Raleigh. The lectoallotype female, here designated, from Waldoboro, Maine, collected by J. H. Lovell, August 26, on *Solidago* sp., is deposited with the holotype, but belongs to the next species described. Two paratypes (male and female) from Waldoboro collected by J. H. Lovell as follows: male, July 23, on *Epilobium angustifolium* and female, August 3, 1905, on *Solidago* sp.,

are in the collection of the Natural History Museum of the University of Colorado at Boulder. These last two also seem to belong to the next described species, rather than to *M. illata.*

Distribution. In Canada from Prince Edward Island west to Alberta and in the United States south to North Carolina and Illinois (Fig. 29). This species has been collected from July 7 to September 19, chiefly in August. In addition to the type material, 146 females and 60 males have been examined from the localities listed below (one female and two males from Colton, California, Pilate collector, are considered to be mislabeled).

CONNECTICUT: Colebrook; Stafford. ILLINOIS: Sheridan. MAINE: Little Deer Island; Mt. Desert; Perry; Saco; Waldoboro; Winthrop. MASSACHUSETTS: Needham. MICHIGAN: Alger Co.; Baraga Co.; Bay City; Bay Co.; Cheboygan; Cheboygan Co.; Delta Co.; Dickinson Co.; Keweenaw Co.; Marquette; Marquette Co.; Midland Co.; Ogemaw Co.; Ontonagon Co.; Pellston (1.5 miles E.); Pontiac; St. Ignace, Mackinac Co. MINNESOTA: Bagley; Basswood Lake, Lake Co.; Duluth; International Falls; Itasca State Park; Kelliher, Beltrami Co.; Pine River; Stewart River, near Lake Superior, Lake Co.; Two Harbors; Vanhorn. NEW HAMPSHIRE: Alstead; Durham; Nelson. NEW YORK: Albany Co.; Garret Hill, Ontario Co.; Greenwood Lake; Ithaca; Keene Valley, Essex Co.; Mt. Whiteface; New Kingston, Delaware Co.; Speculator. NORTH CAROLINA: Highlands; New River. PENNSYLVANIA: Pittsburgh. *Canada.* ALBERTA: Lethbridge; Medicine Hat. MANITOBA: Aweme. NEW BRUNSWICK: Fredericton; Fundy National Park; Nerepis; St. John. NOVA SCOTIA: Cape Breton National Park; Kings Co.; Truro. ONTARIO: Arnprior; Lake of Bays (Norway Point); Muskoka; Orillia; Ottawa; Toronto. PRINCE EDWARD ISLAND: Dalvay House Canadian National Park. QUEBEC: Fort Coulonge; Hull; Kazabazua. SASKATCHEWAN: Love.

Flower Records. Aster sp., *A. azureus, Cirsium arvense, Chrysanthemum leucanthemum pinnatifidum, Grindelia* sp., *Helianthus strumosus, Hieracium aurantiacum, Leontodon* sp., *Rudbeckia serotina, Solidago* sp., *S. canadensis, S. gigantea leiophylla, S. juncea, Sonchus* sp., *Tanacetum vulgare.*

Melissodes (Eumelissodes) subillata, n. sp.

This species is closely related to *M. illata* Lovell and Cockerell, from which it can be distinguished only with some difficulty. The female of *subillata* is like *illata* in coloration and in sculpture but

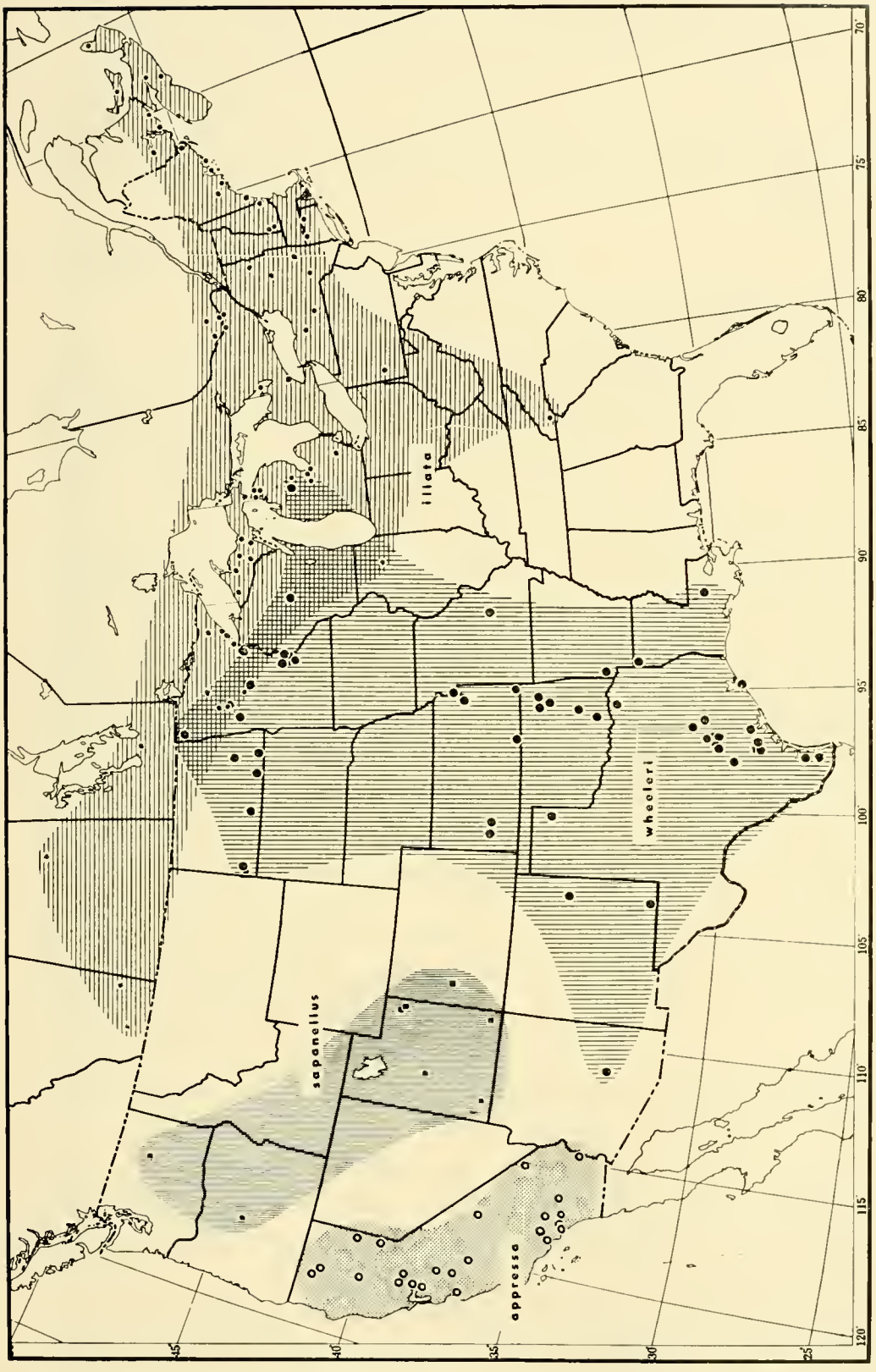


FIG. 29. Map showing the known distributions of *M. (Eumelissodes) illata* Lovell and Cockerell, *M. (E.) wheeleri* Cockerell, *M. (E.) saponellus* Cockerell, and *M. (E.) appressa* LaBerge.

has the galeae more often tessellate, the mesepisterna usually shiny, and the apicomedian area of tergum 4 without minute punctures. The male of *subillata* can be distinguished from that of *illata* by the longer first flagellar segments as described below.

Female. Measurements and ratios: N, 20; length, 9-12 mm.; width, 3.0-4.5 mm.; wing length, M = 3.29 ± 0.197 mm.; hooks in hamulus, M = 12.55 ± 0.256; flagellar segment 1/segment 2, M = 1.98 ± 0.033.

Structure and color: Integumental color as in *illata* except as follows: wing membranes usually somewhat infumate, yellowish brown; tergum 1 with apical fourth or less rufescent.

Structure and sculpture as in *illata* except as follows: galeae above usually dulled by fine tessellation in at least apical half; maxillary palpal ratio about 8.0:6.5:5.3:1.0; lateral areas of vertex with punctures usually separated by one to two puncture widths; mesoscutal punctures usually more crowded peripherally, surface only occasionally dulled by reticular shagreening; mesepisterna with punctures deep and surface usually unshagreened; tergum 1 with punctures of basal half or slightly more shallow, small, apical area and apicolateral lobes impunctate; tergum 4 with apicomedian area beneath pubescence or brown hairs impunctate and dulled as in apical areas of terga 2 and 3; terga 1-4 with apical areas opaque, dulled by dense fine reticulotransverse shagreening.

Hair: Color of vestiture as in *illata* except as follows: in general with less black or dark brown hairs; western specimens (North Dakota) paler; palest without brown on labrum and clypeus, with posteromedian mesoscutal dark patch less than twice size of scutellar dark patch, without brown on lower mesepisterna, with tergum 2 with distal white band narrowly interrupted and tergum 4 without dark brown pubescence apicomedially; darkest specimens as in *illata* but tergum 4 with apicomedian dark area longer and less broad; usually without brown on posterior pronotal lobes, mesepisterna or labrum.

Male. Measurements and ratios: N, 20; length, 9-12 mm.; width, 2.5-4.0 mm.; wing length, M = 3.00 ± 0.181 mm.; hooks in hamulus, M = 11.20 ± 0.247; flagellar segment 2/segment 1, M = 5.59 ± 0.186.

Structure and color: Integumental color as in *illata.* Structure as in *illata* except as follows: minimum length first flagellar segment equals one-seventh or more of maximum length second segment, flagellum reaching beyond pterostigma in repose; maxillary palpal

ratio about 7:5:5:1, fifth segment rarely present. Sculpturing as in female but terga 4 and 5 with apical areas as in 2 and 3. Terminalia as in *illata* but gonostyli not capitate or only slightly so (Figs. 99-101).

Hair: Color of vestiture as in *illata* except as follows: occasionally without brown on vertex and tegulae; mesoscutal dark patch usually about equal to scutellar in size; tergal distal white bands usually broader, that of terga 2 and 5 usually narrowly interrupted medially, but often not.

Bionomics. M. subillata is also an oligolege of the family Compositae. However, the flower data are too sparse and scattered to provide any secure hypothesis regarding generic preferences. Out of 34 collections of bees (48 females and 20 males), 28 are from composites (42 females and 18 males).

Type Material. Holotype female, allotype male, and eight female and six male paratypes from Ann Arbor, Michigan, were collected by L. H. Shinners, June 17, 1952, on *Gaillardia aristosa.* One female and two male paratypes collected by L. H. Shinners at Ann Arbor, Michigan, are as follows: 1 female and 1 male, on *Coreopsis lanceolata,* June 17, 1952; 1 male, on *Coreopsis grandiflora,* June 17, 1952. The holotype and allotype are in the Snow Entomological Museum of the University of Kansas, Lawrence. Paratypes are in the Snow Entomological Museum, the U. S. National Museum, and in the author's collection.

Distribution. M. subillata ranges from Quebec to Saskatchewan in southern Canada and south to North Carolina and Illinois in the United States (Fig. 30). It has been collected from June 1 to September 6, most often in July. In addition to the type material, 130 females and 66 males have been examined from the localities listed below.

Connecticut: Colebrook; Wallingford. Illinois: Carlinville; Downers Grove; Palos Park; South Maywood. Indiana: Greenfield; Lafayette. Maine: Lincoln Co.; South Portland; Southwest Harbor; Waldoboro. Michigan: Ann Arbor; Arenac Co.; Cheboygan; Clinton Co.; Douglas Lake; East Lansing; Eaton Co.; Midland Co.; Oakland Co.; Oceana Co.; Pelee Island. Minnesota: Fergus Falls; Hennepin Co.; Luverne, Rock Co.; Minneapolis; Pelican Lake; Nisswa; Ramsey Co.; Sedan; University Farms, St. Paul. New Jersey: Alpine; Mashipacona, Sussex Co.; Palmyra; Ramsey; Rocky Hill; Tenafly. New York: Albany; Buffalo; Flatbush; Glen Island; Ithaca; Lancaster; McLean; Pelham; Pike. North Carolina: Ashe

Co. (Scenic Highway); Linville Falls; McDowell Co. (Blueridge Parkway); Pender; Southern Pines; Wilmington. NORTH DAKOTA: Dickinson; Fargo; Marmarth; Stanley; Tappen; Valley City. OHIO: Columbus; Franklin Co.; Lakeside, Ottawa Co. OKLAHOMA: South McAlester. SOUTH DAKOTA: Gettysburg. VERMONT: Rutland. VIIRGINIA: Rocky Run, Fairfax Co.; Savannanoa. WISCONSIN: Cedar Lake, Washington Co. *Canada.* MANITOBA: Teulon. NOVA SCOTIA: Cape Breton National Park. ONTARIO: Brockville; Grand Bend; Jordan; Marmora; Ottawa; Pelee Point; Strathroy; Toronto. QUEBEC: Ste. Anne. SASKATCHEWAN: Love.

Flower Records. Aster sp., *A. azureus, Chrysanthemum leucanthemum, Cichorum intybus, Cirsium arvense, Coreopsis* sp., *C. grandiflora, C. lanceolata, Echinacea pallida, Epilobium angustifolium, Eupatorium maculatum, Gaillardia aristata, Helianthus maxillianus, H. petiolaris, Hieracium aurantiacum, Lactuca pulchella, Petalostemum oligophyllum, Platycodon grandiflorium, Psoralea lanceolata, Ratibida columnaris, Rudbeckia* sp., *R. hirta, R. laciniata, Solidago* sp., *S. graminifolium, Sonchus* sp., *S. arvensis glabrescens, Teucrium occidentalis, Vernonia fasciculata.*

Melissodes (Eumelissodes) wheeleri Cockerell

Melissodes wheeleri Cockerell, 1906, Trans. Amer. Ent. Soc., vol. 32, p. 111; 1906, Ann. Mag. Nat. Hist., ser. 7, vol. 17, p. 367.

This species is very closely related to *subillata* and to *illata.* The female of *wheeleri* is like that of *subillata* in sculpture and vestiture, but is paler on the average and the fourth tergum has an apical fringe of black hairs rather than an apicomedian triangle of dark hairs. The male is like *subillata* in sculpture, but has the short first flagellar segments of *illata.* The male of *wheeleri* is distinctive in that the pale hair of the head and thorax is often ochraceous and the mandibles have yellow basal maculae.

Female. Measurements and ratios: N, 20; length, 10-12 mm.; width, 3.5-4.5 mm.; wing length, $M = 3.19 \pm 0.172$ mm.; hooks in hamulus, $M = 12.45 \pm 0.198$; flagellar segment 1/segment 2, $M = 1.86 \pm 0.025$.

Structure and color: Integumental color as in *illata* except as follows: flagellar segments 3-10 and usually apex of 2 red below; wing membranes clear. Structure and sculpture as in *illata* except as follows: supraclypeal area and lateral vertex areas usually shiny and unshagreened or delicately so; galeae above usually with delicate reticular shagreening but scarcely dull; maxillary palpal ratio

about 3.5:2.5:2.5:1.0; mesoscutum with posteromedian area punctures separated mostly by one to two puncture widths; mesepisterna usually unshagreened; metasomal terga sculptured as in *subillata;* pygidial plate as in *illata.*

Hair: Vestiture in general as in *illata* except as follows: posteromedian mesoscutal dark area twice size of scutellar dark area or larger, in darkest forms thorax almost entirely black; posterior lobes of pronotum usually and upper mesepisterna often with black intermixed with white; mesepisterna with ventral, lower anterior and often lower lateral surfaces with brown hairs; tergum 1 with apical area glabrous or with sparse, minute, appressed, brown hairs basally; tergum 2 with distal white band interrupted medially; tergum 4 with apical margin fringed with black pubescence in at least median third; tergum 5 without lateral pale tufts; sternal hairs brown, occasionally pale laterally; legs as in *illata.*

Male. Measurements and ratios: N, 20; length, 8-11 mm.; width, 2.5-3.5 mm.; wing length, M = 3.10 ± 0.185 mm.; hooks in hamulus, M = 11.25 ± 0.236; flagellar segment 2/segment 1, M = 8.20 ± 0.160.

Structure and color: Integumental color as in *illata* except as follows: labrum cream-colored with brown margin; mandibles with yellow basal maculae (often much reduced in size); flagellar segments 2-11 yellow to red below, segment 1 often red also; wing membranes clear, veins reddish brown to dark brown; terga with apical areas usually opaque, piceous or slightly rufescent except tergum 1 hyaline, in northern specimens apical areas often hyaline but infumate at least basally near pubescent bands.

Structure as in *illata* except as follows: minimum length first flagellar segment one-eighth or less of maximum length second segment; maxillary palpal ratio about 3.5:2.5:3.0:1.0, minute fifth segment occasionally present. Sculpturing as in female but tergum 1 with minute punctures to within one-fifth of apex and terga 4 and 5 similar to tergum 3. Terminalia as in *illata.*

Hair: Pale hairs often bright ochraceous or pale rufescent, dark hairs usually reddish brown. In general vestiture as in *illata* but tergum 2 with pale distal band usually broadly interrupted medially, terga 3 and 4 with pale distal bands usually narrowly interrupted, tergum 5 with pale distal band complete, and pale northern specimens with mesoscutal dark hairs reduced to a few or several.

Variation. Two females from Baton Rouge, Louisiana, collected by E. C. VanDyke, October 9, 1939, are quite different in having

the head and thoracic hairs almost entirely black, tergum 4 with apical dark fringe more extensive and encroaching on the distal pale band, galeae densely tessellate above, and the supraclypeal area dulled by fine tessellation. These are here considered to be merely variants of *wheeleri* and represent the darkest form from the southeastern part of the range of the species. The palest specimens are found in New Mexico, North Dakota and Minnesota and a more or less smooth cline is believed to exist between these extremes in at least the degree of melanism of the vestiture.

Bionomics. *M. wheeleri* is an oligolege of the family Compositae and seems to prefer the genera *Gaillardia, Helianthus* and *Rudbeckia* in that order. Out of 42 collections (48 females and 51 males) with flower data, 34 collections (40 females and 46 males) are from composites.

Type Material. Holotype female of *wheeleri* from Fedor, Lee Co., Texas, collected by G. Birkmann, May 23, 1902, is in the collection of the Museum of Natural History of the University of Colorado at Boulder.

Distribution. *M. wheeleri* ranges from Arizona to Louisiana and north to North Dakota and Michigan (Fig. 29). It has been collected from April 17 to October 9, but chiefly in May and June. In addition to the holotype, 64 females and 97 males have been examined from the localities listed below.

ARIZONA: Kelvin. ARKANSAS: DeQueen. KANSAS: Arkansas City; Baxter Springs; Garden City (7 miles E.); Lakin; Lawrence; Leavenworth; Reno, Leavenworth Co. LOUISIANA: Baton Rouge; Ida. MICHIGAN: Roscommon Co. MINNESOTA: Anoka Co.; Cloquet; Crystal Lake (near Robbinsdale); Detroit Lakes; Hennepin Co.; Itasca State Park; Kittson Co.; Pelican Lake; St. Anthony Park, St. Paul; Sucker Lake, Ramsey Co.; University Farm, St. Paul. MISSOURI: Meramec River (S. of State Highway 8). NEW MEXICO: Loving; Tucumcari. NORTH DAKOTA: Cannon Ball; Logging Camp, Slope Co.; Marmarth; Monango; Nicholson; Valley City. OKLAHOMA: Atoka; Claremore; South McAlester; Strang; Wagoner. TEXAS: Bastrop; Bexar Co.; Brazos Co.; Canadian; Edna; Fedor, Lee Co.; Galveston; Giddings; Goliad (and 16 miles E.); Lee Co.; McDade; Paris; Raymondsville; Robertson Co.; Sarita (21 miles S.); Weser. WISCONSIN: Cranmoor.

Flower Records. *Anthemis cotoula, Asclepias tuberosa, Cleome serrulata, Coreopsis* sp., *Echinacea* sp., *Engelmannia bipinnatifida,*

Gaillardia sp., *G. pulchella, Grindelia squarrosa, Helianthus* sp., *H. annuus, H. debilis, H. petiolaris, Opuntia* sp., *Petalostemum* sp., *P. purpureum, Ratibida columnaris, Rudbeckia* sp., *R. bicolor, R. grandiflora, R. hirta, Silphium asperimum, Sphaeralcea* sp.

Melissodes (Eumelissodes) gelida, n. sp.

This is a pale species of the western great plains region. It is closely related to *M. wheeleri* and *M. subillata* from which it differs primarily in the color of the vestiture. Unlike *wheeleri,* females of *gelida* have red hairs on the inner surfaces of the hind basitarsi and red wing veins. The males of *gelida* are like those of *wheeleri* but have yellow or orange wing veins and little or no brown hair on the metasomal terga.

Female. Measurements and ratios: N, 20; length, 10-12 mm.; width, 3.0-4.5 mm.; wing length, M = 3.57 ± 0.160 mm.; hooks in hamulus, M = 14.05 ± 0.246; flagellar segment 1/segment 2, M = 1.84 ± 0.020.

Structure and color: Integumental color as in *illata* except as follows: flagellar segments 3-10 and apex of 2 red below; eyes gray to bluish gray; wing membranes clear, veins dark red; tegulae often slightly rufescent; tibial spurs white to yellow; tergum 1 usually broadly hyaline apically.

Structure and sculpture as in *illata* except as follows: clypeal punctures slightly smaller, round, often separated by one puncture width especially posteromedially; supraclypeal area with fine reticular shagreening and sparse punctures; galeae shiny, unshagreened or extremely delicately so and in less than apical half; maxillary palpal ratio about 4.5:2.0:3.0:1.0; mesoscutum with posteromedian area punctures irregular in size, some minute, separated mostly by one to three puncture widths, surface often dulled by reticular shagreening; mesepisterna with large crowded punctures, surface shiny; metasomal terga sculptured as in *subillata* and *wheeleri;* pygidial plate relatively narrow, longer than broad, apex rounded.

Hair: Head white with abundant dark brown on vertex. Thorax white except scutellum dark brown fringed with white, mesoscutum with posteromedian dark brown patch usually twice as large as scutellar dark patch (often much smaller and never extending forward at anterolateral angles to surpass level of anterior margins of tegulae); pronotum and mesepisterna without dark hairs. Metasomal tergum 1 with long white hairs basally, glabrous apically;

tergum 2 with basal area white, distal pale band white, narrow, often narrowly interrupted medially, interband zone hairs all or mostly white, erect to suberect, apical area with long, suberect to erect, white to brown (but always with some white) hairs; tergum 3 similar to 2 but basal tomentum brown and distal pale band uninterrupted; tergum 4 with apical white pubescent band often fringed at least medially with pale brown hairs; tergum 5 and usually 6 with lateral white tufts; sterna reddish brown; white laterally. Legs white except as follows: outer surfaces fore and middle tarsi, outer-apical surfaces fore and middle tibiae, and basitibial plates brown; inner surfaces fore and middle tarsi yellow to red; inner surfaces hind basitarsi dark red; inner surfaces hind tibiae yellow; scopal hairs white.

Male. Measurements and ratios: N, 20; length, 9-12 mm.; width, 3-4 mm.; wing length, $M = 3.52 \pm 0.127$ mm.; hooks in hamulus, $M = 12.80 \pm 0.213$; flagellar segment 2/segment 1, $M = 7.97 \pm 0.181$.

Structure and color: Integumental color as in *illata* except as follows: flagellum yellow below, red-brown above; labrum with mediobasal pale spot; mandibles with basal yellow spots but these occasionally reduced or absent; eyes gray to green or bluish gray; wing membranes clear, veins yellow to orange; tegulae piceous; tergal apices hyaline, colorless to yellowish, rarely slightly infumate basally.

Structure as in *illata* except as follows: minimum length first flagellar segment one-eighth or less of maximum length second segment (in allotype first equals about one-tenth of second); maxillary palpal ratio about 3.0:2.5:3.0:1.0, second often equals third. Sculpturing as in female but tergum 1 with small punctures scattered to within one-fifth of apical margin and terga 4 and 5 similar to 2. Terminalia as in *subillata.*

Hair: Head and thorax white. Metasomal tergum 1 white, subappressed long hairs usually not reaching apex medially; tergum 2 white basally, distal pale band white, narrow, often narrowly interrupted medially, interband zone and apical area with hairs long, suberect, white; terga 3-5 similar to tergum 2 but pale distal band boarder, uninterrupted, and progressively closer to apical margins; apical areas terga 2-4 occasionally pale brown in part; terga 6 and 7 white to yellow; sterna yellow medially to white at sides. Legs white except inner surfaces tarsi yellow. Long bristlelike hairs of

terga more abundant and longer than usual in *Eumelissodes* giving the metasoma a peculiar hairy look under low power.

Type Material. Holotype female from 15 miles south of Hyannis, Grant Co., Nebraska, collected by W. E. LaBerge, July 9, 1954, on *Ratibida* sp., is in the collection of the Snow Entomological Museum, University of Kansas, Lawrence. The allotype male from Wallace, Nebraska, collected by R. Roberts, July 3, 1933, is in the collection of the University of Nebraska, Lincoln. In addition, 18 female and 23 male paratypes from western Nebraska are as follows: Brown Co.: 3 males on *Helianthus* sp. and 1 male on *Echinacea* sp., June 21, 1902, J. C. Crawford. Glen, Sioux Co.: 5 females and 1 male, August 9, 1905; 4 females and 2 males, August 10, 1905. Haigler: 1 male, July 9, 1911 on *Helianthus petiolarus,* J. T. Zimmer; 1 female on *Ratibida columnaris,* July 10, 1911, J. T. Zimmer. Halsey: 3 males on *R. columnaris* and 1 male on *Verbena stricta,* July 11, 1909, M. H. Swenk; 1 female on *Lacinaria squarrosa,* July 25, 1912, J. T. Zimmer; 1 male, August 4, 1948, R. R. Dreisbach. Hitchcock Co.: 1 male on *Helianthus* sp., June 24, 1905. Imperial: 1 male on *H. petiolaris,* July 9, 1911, R. W. Dawson; 1 female from 8 miles N., July 9, 1954, W. E. LaBerge; 2 females and 1 male on *H. petiolaris,* July 22, 1911, R. W. Dawson. Jim Creek, Sioux Co.: 2 females and 1 male on *Helianthus* sp., July 26, 1911, M. A. Carricker, Jr. Mitchell: 1 male on *H. petiolaris,* June 30, 1913, L. M. Gates; 1 male, July 3, 1913, 1 male, July 9, 1913, L. M. Gates; 1 male on *H. petiolaris,* July 2, 1914, L. M. Gates. Monroe Canyon, Sioux Co.: 1 female on *Vernonia* sp., August 15, 1908, J. T. Zimmer; 1 male on *H. petiolaris,* July 25, 1911, R. W. Dawson; 1 female, August 7, 1913, R. W. Dawson; 1 female on *R. columnaris,* August 19, 1922, E. J. Taylor. War Bonnet Canyon, Sioux Co.: 1 male on *Argemone* sp., July 23, 1901, M. A. Carricker, Jr. Paratypes are deposited in the collections of the University of Nebraska, the Snow Entomological Museum, R. R. Dreisbach, Midland, Michigan, the U. S. National Museum, Washington, D. C. and in the author's collection.

Bionomics. M. gelida is an oligolege of composites and shows some preference for the genus *Helianthus.* Out of 37 collections (20 females and 55 males) with floral data, 32 (15 females and 30 males) are from some composite, and of these 17 collections (7 females and 14 males) are from *Helianthus.*

Distribution. M. gelida ranges from New Mexico and Texas north to Montana and North Dakota (Fig. 30). It has been collected from

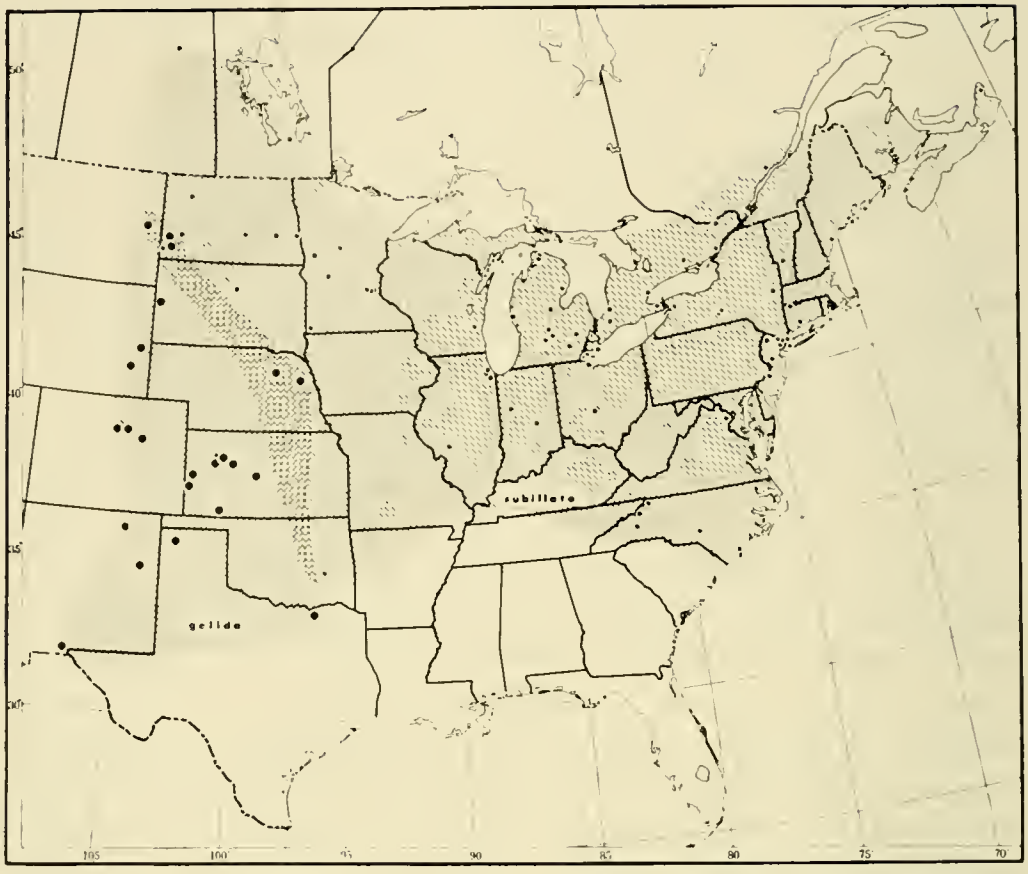


FIG. 30. Map showing the known distributions of *M. (Eumelissodes) gelida* LaBerge and *M. (E.) subillata* LaBerge.

June 3 to August 19, but chiefly in June and July. In addition to the type material, 24 females and 49 males have been examined from the localities listed below (this list does not include the type localities of western Nebraska listed above).

COLORADO: Berkley; Boulder; Brighton; Deer Trail; White Rocks (Valmont). KANSAS: Gove Co.; Great Bend; Hamilton Co.; Meade County State Park; Pierceville; Quinter (5 and 9 miles N.); Trego Co.; Tribune (10 miles E.). MONTANA: Glendive. NEBRASKA: Neligh; West Point. NEW MEXICO: Maxwell; Mesilla; Tucumcari. NORTH DAKOTA: Logging Camp Ranch, Slope Co.; Medora. SOUTH DAKOTA: Custer. TEXAS: Bonham; Dalhart. WYOMING: Lusk; Wheatland.

Flower Records. Argemone sp., *Chrysopsis* sp., *Cosmos* sp., *Echinacea* sp., *Engelmannia pinnatifida, Gaillardia* sp., *Helianthus* sp., *H. annuus, H. petiolaris, Lacinaria squarrosa, Monarda pectinata, Ratibida* sp., *R. columnaris, Sphaeralcea* sp., *Thelesperma gracile, Verbena stricta, Vernonia* sp.

Melissodes (Eumelissodes) subagilis Cockerell

Melissodes agilis var. *subagilis* Cockerell, 1905, Entomologist, vol. 38, p. 145; 1906, Ann. Mag. Nat. Hist., ser. 7, vol. 17, p. 367; 1906, Trans. Amer. Ent. Soc., vol. 32, pp. 76, 92; Snow, 1906, Trans. Kansas Acad. Sci., vol. 20, p. 137; Cockerell, 1923, Ent. News, vol. 34, p. 46; 1925, Ann. Mag. Nat. Hist., ser. 9, vol. 16, p. 229; Brimley, 1938, Insects of North Carolina, p. 462.

Melissodes pecosella Cockerell, 1905, Proc. Biol. Soc. Washington, vol. 18, p. 179 (new synonymy); 1906, Trans. Amer. Ent. Soc., vol. 32, p. 88; 1906, Trans. Amer. Ent. Soc., vol. 32, p. 309; 1906, Ann. Mag. Nat. Hist., ser. 7, vol. 17, p. 366; 1928, Univ. Colorado Studies, vol. 16, p. 114; Cresson, 1928, Mem. Amer. Ent. Soc., vol. 5, p. 69.

Tetraloniella excurrens melanaspis Cockerell, 1925, Ann. Mag. Nat. Hist., ser. 9, vol. 16, p. 228 (new synonymy); Hicks, 1926, Univ. Colorado Studies, vol. 15, p. 225; Cockerell, 1928, Univ. Colorado Studies, vol. 16, p. 114.

Xenoglossodes albertensis Cockerell, 1937, Canadian Ent., vol. 69, p. 87 (new synonymy).

This small species is the first of a series of small pale western species related to the *coreopsis* group. The female of *subagilis* differs from that of *coreopsis* in its pale color, broader distal pale bands of terga 2 and 3, and small size. The male of *subagilis* is very similar to that of *coreopsis* but has the first flagellar segment longer, a broader distal pubescent band on tergum 2, more distinctly punctate terga, and smaller size.

Female. Measurements and ratios: N, 20; length, 9-12 mm.; width, 3.5-4.5 mm.; wing length, M = 2.88 ± 0.185 mm.; hooks in hamulus, M = 11.85 ± 0.194; flagellar segment 1/segment 2, M = 1.94 ± 0.035.

Structure and color: Integument black except as follows: mandibles, legs (at least tarsi) and apical third of tergum 1 usually rufescent; flagellar segments 3-10 and usually apical third or more of 2 yellow to red below, dark brown above; eyes usually blue, occasionally gray or greenish blue; wing membranes clear, veins often dark red, usually reddish brown to black; tegulae piceous, often rufescent above; tibial spurs white to yellowish.

Structure of clypeus as in *coreopsis;* clypeal punctures round, coarse, separated mostly by half a puncture width or less, surface slightly dulled by reticular shagreening; supraclypeal area shiny, unshagreened or delicately so; galeae above usually dulled by dense tessellation in at least apical half; lateral areas of vertex with punctures separated mostly by two to three or more puncture widths, surface shiny; maxillary palpal ratio about 3:2:2:1, rarely a minute fifth segment present. Mesoscutal punctures round, deep, large, peripherally separated by half to one puncture width, posteromedially by two to four widths, often with small posteromedial impunctate area, surface shiny; scutellum similar but punctures

more crowded; mesepisterna with punctures large, deep, separated by half a puncture width or less, surface shiny. Metasomal tergum 1 with round shallow punctures in basal half or slightly more separated by half to one puncture width, apical area impunctate, surface dulled basally by coarse reticulotransverse shagreening, apically less dull, shagreeninng finer; tergum 2 with basal area punctures separated mostly by one to two puncture widths, shiny, interband zone with small sparse punctures separated mostly by two or more puncture widths and of irregular size, surface dulled as in base of tergum 1, apical area impunctate, relatively shiny; terga 3 and 4 similar but interband zone punctures more abundant and apical area usually absent; pygidial plate with rounded apex, longer than broad.

Hair: Head pale ochraceous to white, usually with brown at vertex but usually not abundant. Thorax white laterally to ochraceous above; scutellum often brown with ochraceous peripherally, occasionally entirely pale; mesoscutum in eastern and northern specimens usually with no brown hairs posteromedially or with less than on scutellum, in the southwestern states usually with abundant brown posteromedially but dark patch rarely as much as twice scutellar dark area in size; anterior mesoscutal hairs decumbent; appressed to subappressed. Metasomal tergum 1 with pale ochraceous hairs basally, glabrous apically; tergum 2 white basally, distal pale band pale ochraceous to white, broader than apical apubescent area medially, rarely interrupted medially, apical hairs of pale band relatively simple and about as long as more basal plumose hairs, interband zone hairs short, subappressed to suberect, mostly or entirely ochraceous; tergum 3 similar but basal tomentum brown, distal pale band reaches apex of tergum in at least lateral thirds and usually across entire tergum, tergum 4 with distal pale band apical, white to pale ochraceous, uninterrupted; tergum 5 with broad lateral pale tufts; tergum 6 brown to orange-brown with lateral pale tufts; sterna orange-brown medially to white apicolaterally, white across apex of penultimate sternum. Legs white to pale ochraceous except as follows: outer surfaces fore and middle tibiae brown; inner surfaces hind basitarsi yellow to red in eastern specimens, red to dark reddish brown in western specimen; scopae white.

Male. Measurements and ratios: N, 20; length, 8-11 mm.; width, 2.0-3.5 mm.; wing length, $M = 2.70 \pm 0.196$ mm.; hooks in hamulus, $M = 10.95 \pm 0.235$; flagellar segment 2/segment 1, $M = 6.65 \pm 0.183$.

Structure and color: Integument black except as follows: clypeus yellow except testaceous apical margin and tentorial pits dark; labrum without mediobasal pale spot; mandibles without basal pale spots; flagellum yellow to red beneath, dark red to brown above, segment 1 occasionally entirely brown; eyes usually blue or greenish blue, occasionally gray or yellowish gray; wing membranes clear, veins yellow to dark red, rarely brown; tegulae, tibial spurs, tarsi as in female; terga with apical areas hyaline, colorless to slightly yellowed.

Structure of clypeus as in *coreopsis;* minimum length first flagellar segment equals one-fifth to one-eighth maximum length of second segment, rarely as short as one-tenth second segment, minimum length first segment usually equals more than half its own maximum, flagellum in repose reaching pterostigma, penultimate segment more than three times as long as broad; maxillary palpal ratio about 4.0:3.5:3.0:1.0, minute fifth segment rarely present. Sculpture as in female except as follows: galeae above often only delicately shagreened in apical half or shiny and unshagreened, occasionally densely tessellate as in female; clypeal punctures smaller; tergum 1 with punctures more crowded basally, with small punctures scattered almost to apical margin; tergum 2 with interband zone punctures larger, separated mostly by two puncture widths; terga 3-5 similar to 2, but apical areas progressively shorter. Terminalia as in *agilis,* sternum 8 with ventral tubercle with apex bidentate (Figs. 102-104).

Hair: Head usually ochraceous, occasionally white (especially in western specimens). Thorax white to pale ochraceous laterally, ochraceous dorsally (white dorsally in western specimens), without brown. Metasomal tergum 1 with long white to ochraceous hairs, near apex hairs appressed and surpassing margin but not highly branched and not hiding margin except at extreme sides; tergum 2 with distal pale band usually longer medially than apical apubescent area, apical area with long, relatively simple, white to yellow, subappressed to suberect hairs, without brown; terga 3-5 similar but distal pubescent band progressively closer to apex until tergum 5 without apical area; terga 6 and 7 dark ochraceous to white; sterna yellowish medially to white laterally. Legs white to pale ochraceous except inner surfaces tarsi yellow.

Geographical Variation. The populations from east of the continental divide from North Dakota to New Mexico can be separated in the female sex from those west of the divide. The eastern popu-

lations have females with the pale vestiture primarily ochraceous, with hairs of the inner hind basitarsi orange to red, and with the wing veins reddish brown. From west of the divide females usually have the pale vestiture white, have dark brown wing veins, and the hairs of the inner surfaces hind basitarsi dark reddish brown to almost black. Some exceptions to this distribution of characters occur. A number of females from Utah have pale yellow wing veins and yellowish orange hairs on inner surfaces hind basitarsi.

In the respects listed above about half of the females from Arizona are in the western group, slightly less than half are of the eastern type, and a few intermediates occur. Intermediates occur also in the few specimens available from Alberta, Canada. The remaining females from Alberta are typically eastern except the holotype female of *albertensis* which is of the western type. The name *albertensis* has priority over other available names and would thus apply as a subspecific name for the populations west of the continental divide. The Alberta and Arizona populations would be considered as intermediate groups between the subspecies.

The Arizona females, especially, and some Utah and New Mexico females have dark brown hairs on the mesoscutum. This is rare in the more northern populations. A third subspecies could thus be recognized and, perhaps, a fourth in the southern areas of the range.

The males cannot be so neatly classified into geographic races as the females. The western populations are on the average paler in color, but this characteristic is not reliable as many specimens become faded with age. There are males from Utah which have pale yellow wing veins and flagella from the same localities, in some cases, as the females mentioned above. These are probably much faded specimens in both sexes.

This author is not formalizing the geographic races of *subagilis* with subspecific names because of the nature of the characteristics involved, that is, color which is liable to fading with age, because only one sex is involved, and because one character (dark mesoscutal patch) is not concordant with the others.

Bionomics. Hicks (1926) has described a nesting female of this species found in Colorado (as *Tetraloniella excurrens melanaspis*). The entrance to the burrow was found on level ground in a stand of rattlesnake grass. A female was seen entering and, after a wait of twenty minutes, the nest was excavated. The burrow went straight

into the ground for three inches but no pollen or cell was found at the bottom. This was probably a nest which had only been begun.

M. subagilis is an oligolege of the composite genus *Grindelia.* This is clearly indicated by the floral data accompanying specimens which is summarized in Table XVI.

Type Material. The male holotype of *agilis subagilis* from Fort Collins, Colorado, is in the collection of Prof. P. H. Timberlake, Citrus Experiment Station, Riverside, California. The holotype female of *pecosella* from Pecos, New Mexico, collected by W. P. Cockerell, is in the collection of the Philadelphia Academy of Sciences, Philadelphia, Pennsylvania. The holotype female of *Tetraloniella excurrens melanapsis* from Wray, Colorado, collected by F. E. Lutz, August 17-18, 1919, is in the collection of the American Museum of Natural History, New York City. The holotype female

Fig. 31. Map showing the known distributions of *M. (Eumelissodes) subagilis* Cockerell and *M. (E.) moorei* Cockerell.

of *Xenoglossodes albertensis* from Milk River, Alberta, Canada, collected by W. P. Cockerell, is in the American Museum of Natural History, New York City.

Distribution. *M. subagilis* ranges from northern California, north to Alberta, Canada, east to Minnesota and Iowa, and south to Texas and New Mexico (Fig. 31). It is primarily a Great Plains and Intermontane Region species. It has been collected from June 6 to November 3, but chiefly in July, August and September. In addition to the type material, 455 females and 348 males have been examined from the localities listed below (including the type localities).

TABLE XVI. Summary of Floral Data for *Melissodes subagilis.*

Plant Data			Records of *M. subagilis*			
FAMILY	Number of genera	Number of species	Number of collections	Number of females	Number of males	Total number of bees
Compositae: *Grindelia* spp.	1	2	59	131	81	212
Aster spp.	1	2	8	18	5	23
Helianthus spp.	1	3	11	6	6	12
Other genera	15	20	34	41	37	78
Other families (4)	7	7	10	6	14	20
Totals	25	34	119	202	143	345

ARIZONA: Arlington; Bisbee (10 and 18 miles W.); Carr Canyon, Huachuca Mts.; Chandler Heights; Chiricahua Mts.; Congress Junction; Continental; Douglas (8 miles N. E.); Faraway Ranch; Hereford; Holbrook; Laveen, Moencopi Wash; Nogales; Pearce; Pedersons Ranch (road to), Huachuca Mts.; Phoenix; Picacho Pass; Portal (1 mile W.); Prescott; Ramsey Canyon, Huachuca Mts.; Rock Springs, Yavapai Co.; Sonoita (10 miles E.); Tempe; Theba; Tombstone (4 miles N. W.); Tucson; Turner; Willcox; Yuma. CALIFORNIA: Gazelle, Siskiyou Co. COLORADO: Boulder; Craig; Crook; Denver; Fort Collins; Hoehnes (N. E. of); Limon; Logan Co.; Red Wash; San Luis Valley; Sterling; Timnath; Utah Junction; Wray. IDAHO: Franklin; Hazelton (3 miles N. E.);

Twin Falls. Iowa: Sioux City. Kansas: Cullison; Johnson (2 miles N.), Stanton Co.; Lakin (4 miles E.); Lane Co.; Riley Co.; Smith Co. Minnesota: Luverne; Moorhead; Powder Plant Woods, Ramsey Co.; Ramsey Co.; St. Paul; University Farm, St. Paul. Nebraska: Crawford; Glen, Sioux Co.; Gordon, Sheridan Co.; Lincoln; Lodgepole; McCool Junction; Nebraska City; Omaha; West Point. Nevada: Elko; Pequop (Summitt) Wells, Elko Co. New Mexico: Albuquerque; Algodones; Gallup; Rowe; San Jose; Santa Fe; Tecolote. North Dakota: Belfield; Bismarck; Carpio; Dickinson; Fargo; Glen Ullin; Hatton; Lisbon; Mandan; McKenzie; Minot; Mott; Schafer; Sentinel Butte; Valley City; Williston. Oregon: Ontario; Silver Lake. South Dakota: Ardmore; Cedar Canyon, Badlands; Custer; Deadwood; Hill City (8 miles N.); Hot Springs; Platte; Redfield. Texas: Clarendon; Dallas; Fabens. Utah: Bear River City; Beaver; Benson; Bert; Cache Junction; Collinston; Delta; Elgin; Ephraim; Erda; Farmington; Fort Hall; Garfield; Garland; Glendale; Granite Peak, Dugway Proving Ground, Tooele Co.; Grantsville; Green River; Hanksville (10 miles S.); Hatch; Iosepa; Johnson; Kaysville; Lake Point; Lampo; Logan; Logan Canyon; Payson; Petersboro; Promontory; Saltair Beach; Salt Lake City; Santa Clara; Simpson Springs, Dugway Proving Ground, Tooele Co.; Skull Valley; Smelter; Delle; Timpie; Tooele. Washington: Coulee City. Wyoming: Carbon Co.; Douglas; Flat Creek; Jackson Hole; Niobrara Co. (northern part); North Campbell Co.; Old Woman Creek, Niobrara Co. *Canada.* Alberta: Lethbridge; Magrath; Medicine Hat; Milk River; Scandia; Welling.

Flower Records. Aplopappas sp., *A. gracilis, A. spinulosus, A. tenuisectus, Aster* sp., *A. adscendus, Baccharis* sp., *Baileya* sp., *B. multiradiata, Bigelovia wrightii, Chrysopsis* sp., *C. hispida, Chrysothamnus* sp., *C. viscidiflorus, Cleome* sp., *C. serrulata, Erigeron* sp., *Gossypium herbaceum, Grindelia* sp., *G. nana, G. squarrosa, Gutierrezia sarothrae, Helianthus* sp., *H. annuus, H. maximillianus, H. petiolaris, Heterotheca subaxillaris, Isocoma acradenia, Medicago sativa, Pectis papposa, Petalostemum* sp., *Prionopsis ciliata, Ratibida tagetes, Salsola pestifer, Silphium* sp., *Solidago* sp., *S. rigida, S. serotina, Sphaeralcea* sp., *Verbena hastata, Verbesina* sp., *V. exauriculata.*

Melissodes (Eumelissodes) limbus, n. sp.

This is a small species from southwestern United States and Mexico. It is related to *subagilis,* although not closely. Both male and female of *limbus* are unlike *subagilis* in that the apical

areas of the terga have short, brown, relatively simple, subappressed to suberect hairs.

Female. Measurements and ratios: N, 20; length, 9-11 mm.; width, 3-4 mm.; wing length, M = 2.83 ± 0.111 mm.; hooks in hamulus, M = 11.90 ± 0.164; flagellar segment 1/segment 2, M = 1.99 ± 0.024.

Structure and color: Integument as in *subagilis* except as follows: eyes blue; wing veins dark brown to black; tegulae often rufescent.

Structure and sculpture as in *subagilis* except as follows: clypeal punctures irregular in size, larger posteriorly, separated mostly by half a puncture width, apicomedian carina often broad and punctate, surface shiny, with no or extremely delicate shagreening; supraclypeal area punctate, shiny; galeae above shiny, unshagreened except near tips; maxillary palpal ratio about 4.0:2.5:2.5:1.0. Mesoscutal punctures small, round, peripherally separated by half to one and posteromedially by half to three puncture widths, surface shiny, unshagreened or delicately so; mesepisternal punctures separated by less than half to one puncture width, mostly by about one-half. Metasomal tergum 1 with shallow punctures in basal three-fifths separated mostly by half to one puncture width; tergum 2 with basal area punctures small, separated mostly by one puncture width or less, interband zone punctures minute, shallow, separated by one to three puncture widths, apical area with sparse minute punctures no more than twice width of hairs arising from them, surface moderately shiny to shiny; tergum 3 similar to 2 but apical area punctures reduced to one or two rows just apical to distal white band; tergum 4 similar but apical area absent; pygidial plate V-shaped, not much rounded apically, longer than broad.

Hair: Head white except vertex with relatively sparse long brown hairs (absent in allotype). Thorax white laterally; mesoscutum white to pale ochraceous except posteromedial brown patch which extends forward to a transverse line at about middle of tegulae; scutellum dark brown medially, white peripherally; tegulae without brown. Tergum 1 white basally, glabrous apically except at extreme sides; tergum 2 white basally, distal pale band white, as long as apical apubescent area medially, usually not interrupted medially, although usually thinned, interband zone hairs short, simple, subappressed to suberect, dark brown, apical area with similar hairs but longer; tergum 3 similar to 2 but distal pale band broader and apical area shorter, apical brown hair fringe often worn away; tergum 4 with distal white band apical, uninterrupted;

terga 5 and 6 dark brown medially, with distinct white lateral tufts; sterna reddish brown medially to white laterally, penultimate sternum white apically. Legs white except as follows: outer surfaces fore tarsi and outer apical surfaces fore and middle tibiae light brown; basitibial plate brown; inner surfaces basitarsi yellow to red; inner surfaces hind tibiae yellow.

Male. Measurements and ratios: N, 20; length, 9-11 mm.; width, 2.5-3.5 mm.; wing length, M = 2.86 ± 0.138 mm.; hooks in hamulus, M = 11.05 ± 0.198; flagellar segment 2/segment 1, M = 9.00 ± 0.286.

Structure and color: Integument color as in *subagilis* except as follows: base of mandibles (holotype) occasionally with yellow spots; labrum occasionally with mediobasal yellow spots; flagellar segment 1 yellow; wing veins red to reddish brown; tegulae usually testaceous.

Structure as in *subagilis* except as follows: minimum length first flagellar segment equals one-tenth maximum length second segment and usually half of its own maximum length, flagellum reaches middle of submarginal cell or beyond in repose; maxillary palpal ratio about 3.0:2.5:2.5:1.0. Sculpture as in female except as follows: tergum 1 with scattered minute punctures to within one-sixth of apical margin; terga 2 and 3 with apical areas impunctate; terga 3-5 with interband zones with distinct round punctures separated by one puncture width or less, with apical areas progressively shorter. Terminalia as in *agilis,* sternum 8 with tubercle bidentate apically.

Hair: Head white. Thorax white laterally; white to pale ochraceous dorsally; scutellum and mesoscutum without brown. Tergum 1 usually white to pale ochraceous, apically with shorter, relatively simple, appressed to subappressed, pale hairs reaching or surpassing apical margin but not obscuring apical area except at extreme sides; terga 2-7 as in *subagilis* except as follows: 2 and 3, often 4, with apical areas with short, relatively simple, subappressed to suberect, pale to dark brown hairs, terga 4 and 5 occasionally with pale brown in interband zones, and terga 6 and 7 ochraceous to pale brown. Sterna and legs as in *subagilis.*

Bionomics. This species is an oligolege of composites and seems to prefer the genera *Verbesina, Aplopappus,* and *Baileya* in that order. However, the available floral data are not complete enough to make a more precise statement of preference. It is worthy of remark that *M. limbus* has not yet been collected on *Helianthus,*

a genus frequented by most *Eumelissodes*. Also, large numbers, mostly males, have been taken on *Melilotus alba* at the American Museum of Natural History Southwest Research Station near Portal, Arizona.

Type Material. The holotype male and nineteen male paratypes from 10 miles south of Tucson, Arizona, collected by C. D. Michener, August 7, 1940, on *Verbesina* sp., are in the Snow Entomological Museum of the University of Kansas, Lawrence. The allotype female from Tucson, collected by G. D. Butler, May 14, 1955, on *Baileya multiradiata,* is in the collection of the University of Arizona at Tucson. In addition to the above, 18 female and 42 male paratypes from Tucson, Arizona, or the immediate vicinity, are as follows: 1 male, October 2-25, 1916; 1 female, September, 1930, Frances Hamilton; 1 female, September 16, 1932, R. A. Flock; 1 female, April 1, 1934, Bryant; 1 male, August 17, 1937, R. H. Crandall; 1 male on *Sphaeralcea* sp. and 25 males on *Verbesina exauriculata*, August 7, 1940, P. H. Timberlake; 2 males, August 7, 1940, C. D. Michener; 6 males, August 7, 1940, E. S. Ross; 1 male, April 27, 1951, K. L. Dyre; 1 female on desert marigold and 1 female without floral data, May 11, 1953, G. D. Butler; 2 females and 1 male, May 12, 1953, G. D. Butler, 1 female, May 28, 1953, G. D. Butler; 2 females on *Verbesina* sp., May 29, 1953, G. D. Butler; 1 female, October 4, 1953, G. D. Butler; 1 female on *Aplopappus* sp., May 30, 1954, F. G. Werner; 1 male on *Aplopappus* sp., September 26, 1954, F. G. Werner; 3 females on *Encelia farinosa* and 1 female on *Baileya* sp., G. D. Butler, April 24, 1955; 3 males on *Argemone* sp., F. G. Werner and G. D. Butler, August 24, 1955; 2 females on *Baccharis* sp., October 14, 1955, G. D. Butler. Paratypes are deposited in the collections of P. H. Timberlake, Citrus Experiment Station, Riverside, California, the University of Arizona, the Snow Entomological Museum, the California Academy of Sciences, San Francisco, the U. S. National Museum in Washington, D. C. and in the author's collection.

Distribution. M. limbus ranges from Arizona, southern New Mexico and Texas to Jalisco in Mexico (Fig. 32). It has been collected from April 1 to October 25 with seemingly two peaks of abundance in May and in August. In addition to the type material, 70 females and 161 males have been examined from the localities listed below (the list includes the type locality).

ARIZONA: Apache; Bisbee (10 miles N. W.); Chiricahua Mts.; Continental; Cortaro; Douglas; Drake; Elfrida; Emery Park; Flag-

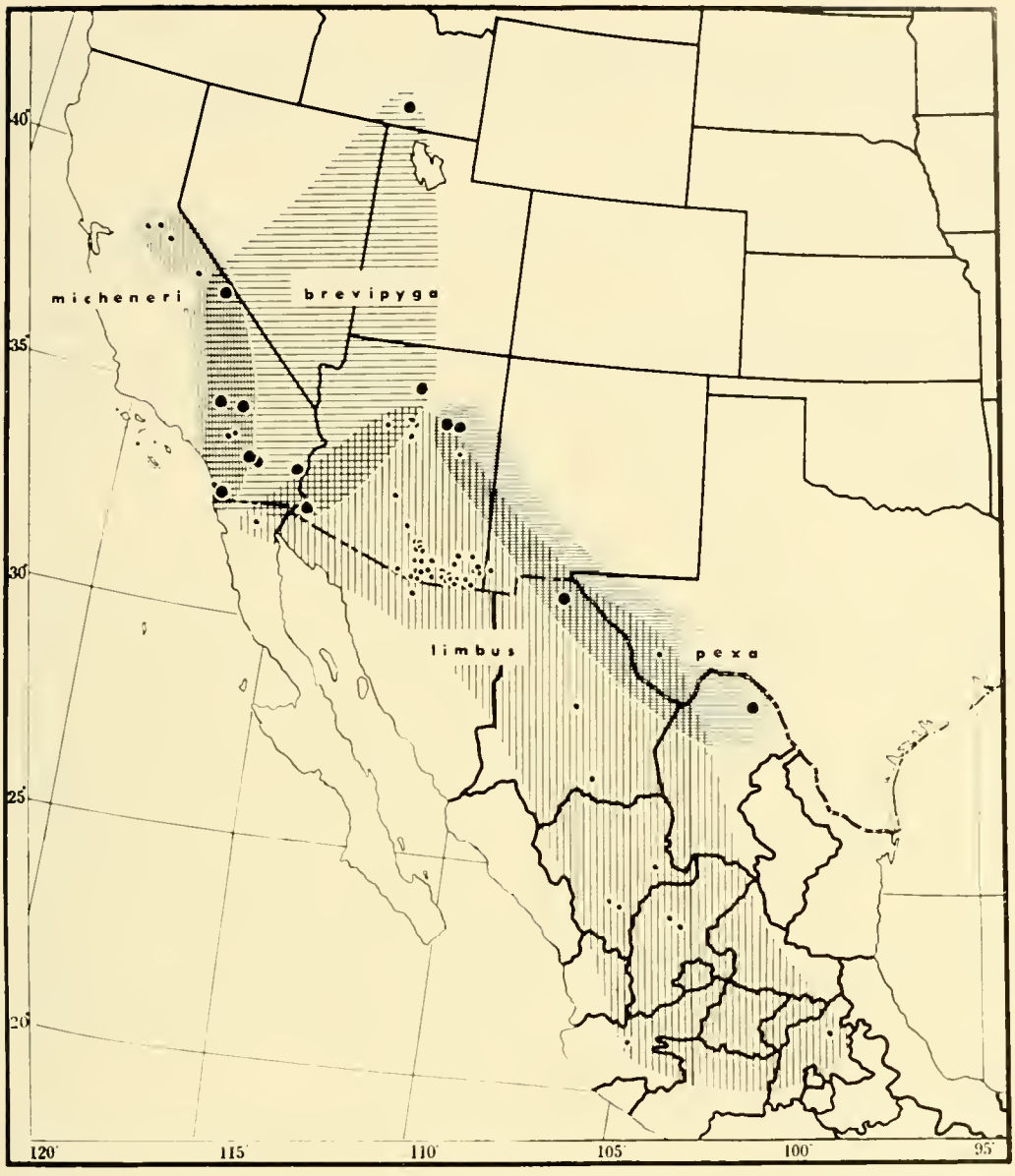


FIG. 32. Map showing the known distributions of *M. (Eumelissodes) limbus* LaBerge, *M. (E.) pexa* LaBerge, *M. (E.) brevipyga* LaBerge, and *M. (E.) micheneri* LaBerge.

staff; Hereford; Huachuca Mts.; Madera Canyon, Santa Rita Mts.; Marana; Nogales; Oak Creek Canyon; Patagonia; Pearce; Petersons Ranch, Huachuca Mts.; Phoenix; Picacho Pass, Pinal Co.; Portal; Ramsey Canyon, Huachuca Mts.; Rillito (12 miles W. on Silverbelt Road); Sahuarita; Santa Rita Mts.; Sasabe; Sedona; Snowflake; Sonoita; Southwest Research Station (5 miles W. of Portal); Sycamore Canyon, Tumacacori Mts.; Tombstone; Tucson; Turner; Vail; Warren; Willcox (2.5 miles S.). NEW MEXICO: Rodeo (10 miles N.), San Simon Valley, Hidalgo Co. TEXAS: Marfa. *México.* BAJA CALIFORNIA: Big Canyon, Sierra Laguna. CHIHUAHUA:

Charcos, Allende District; Chihuahua. DURANGO: Durango; Nombre de Dios; Palos Colorados; Rodeo (12 miles N.); Yerbanis, Cuencamé District. HIDALGO: Actopán. JALISCO: Lagos de Moreno (15 miles N. E.). SONORA: Imuris (12 miles N.). ZACATECAS: Fresnillo; Sain Alto.

Flower Records. *Aplopappus* sp., *A. gracilis, A. spinulosus, A. tenuisectus, Argemone* sp., *Aster* sp., *Baccharis* sp., *Baileya* sp., *B. multiradiata, Chrysothamnus* sp., *Encelia farinosa, Eriogonum* sp., *Gossypium herbaceum, Grindelia* sp., *Gutierrezia* sp., *Hymenothrix wislizenii, Kallstroemia grandiflora, Marrubium vulgare, Melilotus alba, Pectis papposa, Sphaeralcea* sp., *Verbesina* sp., *V. encelioides, V. exauriculata, Wedeliella incarnata.*

Melissodes (Eumelissodes) rufipes, n. sp.

This is a Mexican species which is extremely closely allied to *M. subagilis* of the United States. Indeed, it may prove to be no more than a well-marked geographical race of *subagilis,* but it is here treated as a distinct species until additional evidence clarifies the matter. The female of *rufipes* is similar to that of *subagilis* but is slightly larger, has brown on the mesoscutum and scutellum, and has the distal pale band of tergum 2 narrowly interrupted medially. The male is like that of *subagilis* but has the galeae usually shiny and only slightly shagreened if at all. Both sexes of *rufipes* differ from the typical *subagilis* in that the hair of the head and thorax is longer and more erect, that on the vertex of the male being longer than the third flagellar segment.

Female. Measurements and ratios: N, 20; length, 10-13 mm.; width, 3.5-4.5 mm.; wing length, M = 3.25 ± 0.140 mm.; hooks in hamulus, M = 12.90 ± 0.176; flagellar segment 1/segment 2, M = 2.00 ± 0.025.

Structure and color: Integumental color as in *subagilis* except as follows: apical half of mandible, distitarsi and apical margin of tergum 1 rufescent; flagellar segments 3-10 dark red below, black above, apex of segment 2 occasionally red below, base of segment 3 often red below (allotype); eyes yellowish gray to greenish gray; wing veins dark reddish brown; tegulae black.

Structure and sculpture as in *subagilis* except as follows: clypeus and usually supraclypeal area with surface somewhat dulled by tessellation; galeae reticularly shagreened above in apical half or more, usually shiny basally; maxillary palpal ratio about 4.0:3.5: 3.0:1.0. Mesoscutal surface often (allotype) dulled by reticular

shagreening posteromedially; scutellar punctures smaller and more crowded; mesepisternal punctures equal to posteromedial mesoscutal punctures and separated mostly by less than half a puncture width. Metasomal tergum 1 with basal three-fifths with shallow crowded punctures separated mostly by half a puncture width, apical area impunctate; tergum 2 with basal area punctures separated mostly by one puncture width or less, interband zone punctures minute, separated mostly by one to two puncture widths.

Hair: Color of vestiture as in eastern forms of *subagilis* except as follows: vertex of head with abundant black; scutellum and mesoscutum with black, dark mesoscutal area twice size of scutellar dark area or smaller; tergum 2 with distal pale band usually narrowly interrupted medially; terga 5 and 6 golden to light brown medially and white to ochraceous laterally; legs with inner surfaces hind basitarsi red to orange-yellow. Hairs of head and thorax longer than in *subagilis;* those on anterior part of mesoscutum tend to be erect rather than decumbent as in *subagilis.*

Male. Measurements and ratios: N, 18; length, about 11 mm.; width, about 3.5 mm.; wing length, $M = 3.19 \pm 0.247$ mm.; hooks in hamulus, $M = 11.56 \pm 0.217$; flagellar segment 2/segment 1, $M = 5.93 \pm 0.154$.

Structure and color: Integumental color as in *subagilis* except as follows: eyes yellowish gray to greenish gray; first flagellar segment (holotype) usually entirely brown.

Structure as in *subagilis* except as follows: maxillary palpal ratio about 4.0:3.0:2.5:1.0. Sculpture as in female except as follows: galeae above only delicately shagreened and often only in apical third (holotype) or less; tergum 1 punctate to within one-sixth of apical margin medially, punctures separated mostly by one to two puncture widths; terga 3-5 similar to 2 but apical areas progressively shorter. Terminalia as in *agilis* but sternum 8 with ventral tubercle lamellate with apex acute.

Hair: Vestiture color as in *subagilis* except as follows: in general pale ochraceous; scutellum medially and mesoscutum posteromedially occasionally with brown hairs (not in holotype); tergum 2 with distal pubescent band usually shorter medially than apical apubescent area (subequal in holotype). Hairs of head and thorax longer than in *subagilis;* those of vertex of head usually distinctly longer than flagellar segment 3; those of anterior part of mesoscutum erect to suberect rather than decumbent as in *subagilis.*

Type Material. Holotype male, allotype female, and 21 female and 2 male paratypes from Pachuca, Hidalgo, México, were collected by the University of Kansas Mexican Expedition, June 24, 1953. The holotype and allotype are in the Snow Entomological Museum of the University of Kansas, Lawrence. Paratypes are in the Snow Entomological Museum, the U. S. National Museum, Washington, D. C., and in the author's collection. In addition to the above, four female paratypes from Pachuca, Hidalgo, México, July 28, 1954, and one female and four male paratypes from Actopán, Hidalgo, México, July 29, 1954, were collected by the University of Kansas Mexican Expedition of 1954.

Distribution. M. rufipes ranges through northern Mexico from Chihuahua to Coahuila and south to Hidalgo and Aguascalientes. It has been collected from June 24 to August 21. In addition to the type material, 11 females and 9 males were examined. Localities of these and of the types are listed below.

AGUASCALIENTES: Aguascalientes; Rincon de Romos. CHIHUAHUA: Matachic (2 miles W.); Parrita (19 miles S.). COAHUILA: Cabos. DURANGO: Durango (and 18 miles S.); Nombre de Dios. HIDALGO: Actopán; Pachuca.

Melissodes (Eumelissodes) humilior Cockerell

Melissodes humilior Cockerell, 1903, Ann. Mag. Nat. Hist., ser. 7, vol. 12, p. 447; 1906, Trans. Amer. Ent. Soc., vol. 32, p. 87; 1906, Trans. Amer. Ent. Soc., vol. 32, p. 309; 1906, Ann. Mag. Nat. Hist., ser. 7, vol. 17, p. 286.
Melissodes intermedia, Cockerell (misidentification), 1898, Bull. Sci. Lab. Denison Univ., vol. 11, p. 67; 1898, Bull. Univ. New Mexico, vol. 1, p. 67; 1903, Ann. Mag. Nat. Hist., ser. 7, vol. 12, p. 450.
Melissodes intermediella Cockerell, 1905, Bull. S. California Acad. Sci., vol. 4, p. 102 (new synonymy); 1906, Trans. Amer. Ent. Soc., vol. 32, pp. 88, 92; 1906, Trans. Amer. Ent. Soc., vol. 32, p. 310; 1906, Ann. Mag. Nat. Hist., ser. 7, vol. 17, p. 366; Snow, 1906, Trans. Kansas Acad. Sci., vol. 20, p. 137.

This is a small species closely related to *M. limbus.* The female of *humilior* can be distinguished from that of *limbus* by the broader apical areas of terga 2 and 3 (with dark hairs as in *limbus*), the darker hairs of the inner surfaces of the hind basitarsi, the darker wing veins, and the shagreened galeae. The male of *humilior* can be told from that of *limbus* principally by the large basal triangular yellow spots of the mandibles and the large pale mediobasal labral spot.

Female. Measurements and ratios: N, 20; length, 9-11 mm.; width, 3-4 mm.; wing length, $M = 2.75 \pm 0.197$ mm.; hooks in hamulus, $M = 12.00 \pm 0.205$; flagellar segment 1/segment 2, $M = 1.97 \pm 0.035$.

Structure and color: Integumental color as in *subagilis* except as follows: tergum 1 extremely narrowly hyaline apically, not much rufescent if any; wing veins dark brown to black. Structure and sculpture as in *subagilis* except as follows: clypeus with surface often coarsely shagreened, dull; supraclypeal area usually dulled by reticular shagreening or fine tessellation in apical half or more; maxillary palpal ratio about 3.5:2.5:2.5:1.0, posteromedian mesoscutal punctures usually separated by one to two puncture widths, rarely with subimpunctate area, surface shiny, delicately or not at all shagreened; tergum 1 with basal three-fifths with large shallow punctures separated mostly by less than one puncture width; tergum 2 with basal area punctures separated mostly by half to one puncture width, interband zone with distinct punctures separated mostly by one to two puncture widths, apical area with minute punctures equal to no more than twice diameter of hairs arising from them; pygidial plate V-shaped, well-rounded apically, longer than broad.

Hair: Vestiture in general as in *limbus* except as follows: mesoscutal dark patch often no larger than scutellar; tergum 2 with interband zone with short suberect to subappressed hairs at least partly dark brown; terga 2 and 3 with apical areas of dark brown suberect hairs longer, on tergum 2 distal pale band often no longer medially than apical area, on tergum 3 distal white band often not reaching apex laterally; inner surfaces hind basitarsi with dark brown to black hairs.

Male. Measurements and ratios: N, 20; length, 8-10 mm.; width, 2.5-3.5 mm.; wing length, $M = 2.74 \pm 0.143$ mm.; hooks in hamulus, $M = 10.90 \pm 0.216$; flagellar segment 2/segment 1, $M = 8.52 \pm 0.878$.

Structure and color: Integumental color as in *subagilis* except as follows: labrum with large mediobasal cream-colored spot (equals half or more of total area); mandible with basal triangular yellow spot; first flagellar segment entirely brown; wing veins red to yellow. Structure as in *subagilis* except as follows: minimum length first flagellar segment equals one-eighth to one-tenth maximum length second segment and usually more than half of its own maximum length, flagellum surpassing pterostigma in repose; maxillary palpal ratio about 4.8:2.4:3.2:1.0. Sculpture as in female except as follows: galeae usually shagreened above only near tips, shiny; tergum 1 with scattered minute punctures almost to apical margin; tergum 2 with apical area impunctate; terga 3-5 similar

to 2 but apical areas progressively shorter. Terminalia as in *agilis*, sternum 8 with ventral tubercle blunt, only obscurely bidentate (Figs. 105-106).

Hair: Vestiture color as in *limbus;* however, the specimens before me are mostly much faded and worn so that the apical dark hairs of terga 2-4 are worn away but these are evident in four of the specimens from Texas and New Mexico.

Type Material. Holotype female of *humilior* from Organ, New Mexico, collected by T. D. A. Cockerell, September 28 at 5100 feet elevation, is in the collection of the Natural History Museum of the University of Colorado at Boulder. The holotype female of *intermediella* from Las Cruces, New Mexico, July, is also in the Natural History Museum in Boulder, Colorado.

Distribution. M. humilior is known from Texas, New Mexico, Arizona, and Chihuahua, Mexico (Fig. 33). It has been collected from June 12 to November 3. In addition to the type material, 49 females and 25 males have been examined from the localities listed below.

ARIZONA: Boyce Thompson Arbor, Superior; Chandler Heights; Chiricahua Mts. (2 miles S.); Glove (2 miles W.); Higley; Payson; Phoenix; Randolph; San Xavier Mission; Tucson. NEW MEXICO: Albuquerque; Garfield; Hot Springs; Las Cruces; Malaga (14 miles S.); Mesilla. TEXAS: Davis Mts.; Fort Davis; Santa Elena Canyon, Big Bend National Park; Tuna-Vinton highway, El Paso Co. *Mexico.* CHIHUAHUA: Parral (9 miles S.).

Flower Records. Aster sp., *A. crassulus, A. spinosus, A. tenacetifolius, Grindelia* sp., *Helenium autumnale, Heterotheca* sp., *Isocoma* sp., *I. acradenia, Lygodesmia juncea, Solidago occidentalis, Sphaeralcea emoryi, Verbesina encelioides.*

Melissodes (*Eumelissodes*) *verbesinarum* Cockerell

Melissodes pecosella verbesinarum Cockerell, 1905, Proc. Biol. Soc. Washingington, vol. 18, p. 180; 1906, Trans. Amer. Ent. Soc., vol. 32, p. 88; 1906, Ann. Mag. Nat. Hist., ser. 7, vol. 17, p. 366.

This small species is very closely allied to *M. humilior.* The female of *verbesinarum* is similar to that of *humilior* but has shiny, unshagreened galeae, paler hair on the mesoscutum, and yellow to reddish brown hairs on the inner surfaces hind basitarsi. The male of *verbesinarum* can be told from that of *humilior* only with some difficulty. The *verbesinarum* males have larger yellow maculae on the mandibular bases and have denser, more branched hairs obscuring the apical margin of the first tergum as described below.

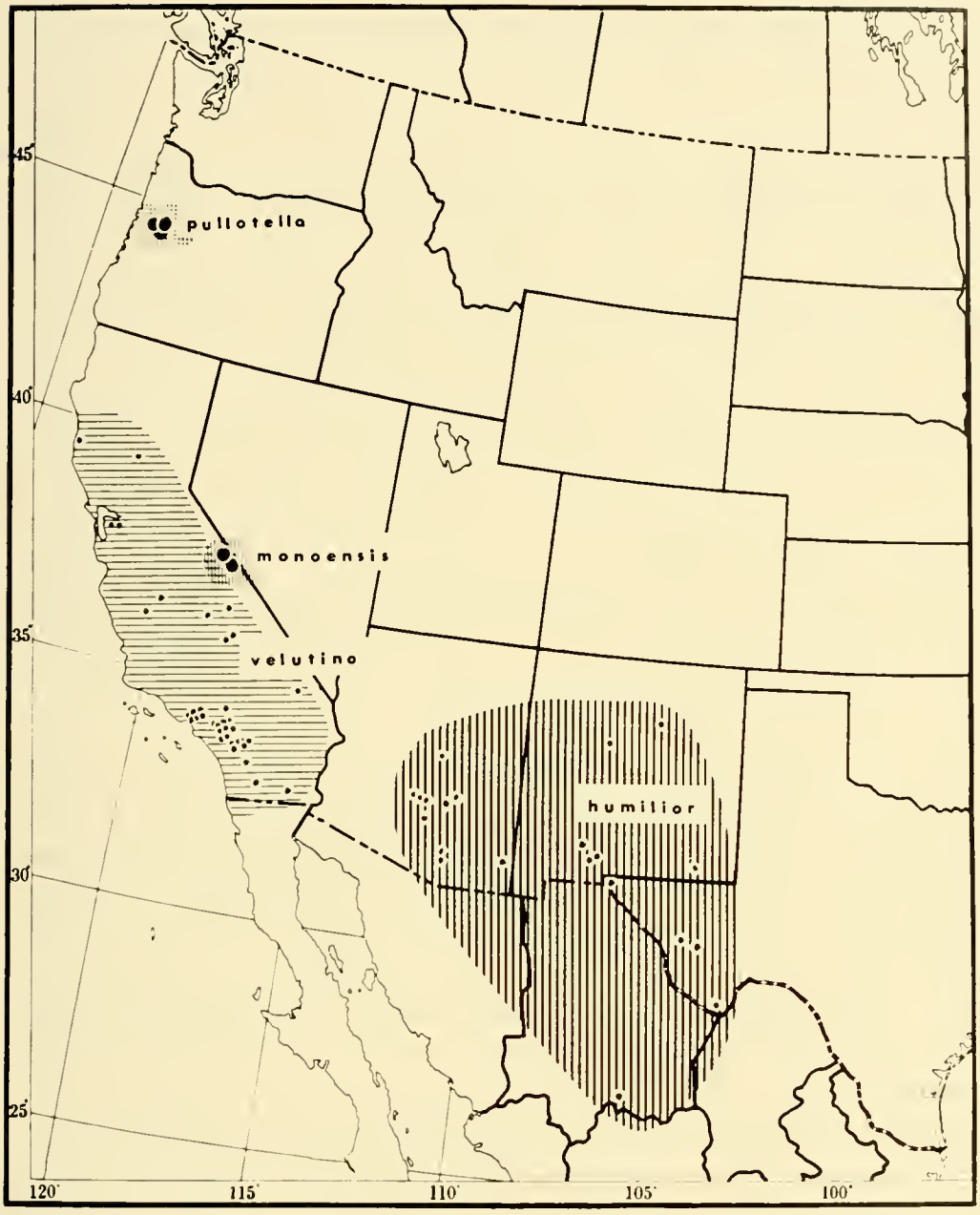


FIG. 33. Map showing the known distributions of *M. (Eumelissodes) pullatella* LaBerge, *M. (E.) monoensis* LaBerge, *M. (E.) velutina* Cockerell, and *M. (E.) humilior* Cockerell.

Female. Measurements and ratios: N, 20; length, 8-10 mm.; width, 2.5-3.5 mm.; wing length, M = 2.84 ± 0.132 mm.; hooks in hamulus, M = 12.20 ± 0.210; flagellar segment 1/segment 2, M = 1.87 ± 0.100.

Structure and color: Integumental color as in *subagilis* except as follows: second flagellar segment entirely black or red below at tip only: eyes gray to grayish blue; wing veins reddish brown to brown; tegulae usually rufescent or testaceous.

Structure and sculpture as in *subagilis* except as follows: eyes larger, in profile about one and one-half as broad as gular area; clypeal punctures coarse, surface shiny, unshagreened or slightly so, apicomedial carina absent or poorly developed; supraclypeal area dulled by irregularly reticular shagreening or shiny; galeae shiny, unshagreened except at tips; maxillary palpal ratio about 2.4:2.0: 2.0:1.0, first segment often slightly longer; posteromedial mesoscutal punctures separated mostly by one to three puncture widths, surface occasionally lightly shagreened; tergum 1 with basal three-fifths with crowded punctures separated mostly by half a puncture width or less; tergum 2 with basal area punctures separated mostly by one puncture width, surface unshagreened, interband zone with small, round, distinct punctures separated mostly by one puncture width or slightly more, surface moderately shiny, reticularly shagreened, apical area absent across most of tergum (except, perhaps, median third or less), if present, impunctate and less than half as long as distal pubescent band medially; tergum 3 similar to but apical area absent or virtually so and interband zone punctures denser; tergum 4 similar to 3.

Hair: Head white, with little or no brown on vertex. Thorax white laterally, dorsally with pale hairs pale ochraceous, scutellum brown fringed with white, mesoscutum with brown posteromedial patch rarely any larger than scutellar dark patch and occasionally all hairs pale ochraceous. Tergum 2 with long white basally, distal pubescent band white, reaching apical margin at least in lateral thirds, longer than interband zone, and uninterrupted medially, interband zone hairs short, subappressed, white with usually some brown mixed in medially; tergum 3 similar to 2 but brown basally and distal pubescent band reaching apex across all or most of tergum; tergum 4 like 3; terga 5 and 6 dark brown with lateral white tufts; sterna golden to reddish brown, white laterally, penultimate segment fringes apically with white. Legs white except as follows: fore tarsi pale brown; outer-apical surface middle tibiae orange-brown; basitibial plates brown; inner surfaces hind basitarsi yellow, red, or reddish-brown; scopae white.

Male. Measurements and ratios: N, 20; length, 9-11 mm.; width, 2.5-3.0 mm.; wing length, $M = 2.71 \pm 0.162$ mm.; hooks in hamulus, $M = 10.80 \pm 0.200$; flagellar segment 2/segment 1, $M = 8.13 \pm 0.143$.

Structure and color: Integumental color as in *subagilis* except as follows: labrum white with brown or testaceous apical border; mandibular base yellow (usually base wholly yellow and not with

triangular yellow area), apical half red; flagellum yellow below, red to brown above, first segment usually entirely red or brown; eyes gray to grayish blue; wing veins yellow to red; tegulae testaceous.

Structure as in *subagilis* except as follows: minimum length first flagellar segment equals about one-ninth maximum length of second, rarely as much as one-eighth; maxillary palpal ratio about 2.4:2.0:2.0:1.0, second segment often slightly longer. Sculpturing as in female except as follows: tergum 1 with minute punctures almost to apical margin; tergum 2 with basal and interband zone punctures often slightly larger and sparser; terga 3-5 as in tergum 3 of female. Terminalia as in *agilis* but sternum 8 with ventral tubercle acute, not bidentate.

Hair: Head and thorax white, occasionally slightly cinereous on dorsum of thorax; metasomal terga as in *subagilis* except as follows: all hairs and pubescence white; tergum 1 with apical area obscured by dense, appressed, short, white barbed hairs; tergum 2 with distal white band always as long medially as apical area or longer. Legs white except inner surfaces tarsi yellow.

Bionomics. *M. verbesinarum* is a composite oligolege, but the available floral data do not show any decided flower preferences within the family Compositae. It is certain that, in spite of its name, *verbesinarum* is not an oligolege of the genus *Verbesina*, although it has been taken on that genus a few times. Out of 61 collections (87 females and 88 males) with floral data, 49 collections (83 females and 76 males) are from some composite.

Type Material. Holotype female of *verbesinarum* from Las Cruces, collected by T. D. A. Cockerell, September 22, on *Verbesina enceliodes*, is in the collection of Prof. P. H. Timberlake, Citrus Experiment Station, Riverside, California.

Distribution. *M. verbesinarum* is known from Washington to southern California and Jalisco, Mexico, and east to Nevada and Texas (Fig. 34). It has been collected from April 25 to November 13, chiefly from June to August. In addition to the holotype, 153 females and 130 males have been examined from the localities listed below.

Arizona: Aguila; Atasocsa Mts.; Benson (and 5 miles W.); Bonita; Brenda (2.3 miles W.); Cameron (20 and 24 miles N.); Chiricahua Mts.; Chino Valley; Cochise; Cork; Elfrida; Eloy (7 miles W. and 8 miles S. W.); Fredonia; Gila Bend (and 25 miles E.); Globe; Higley; Holbrook (15 miles W.); Morenci; Phoenix (N. of);

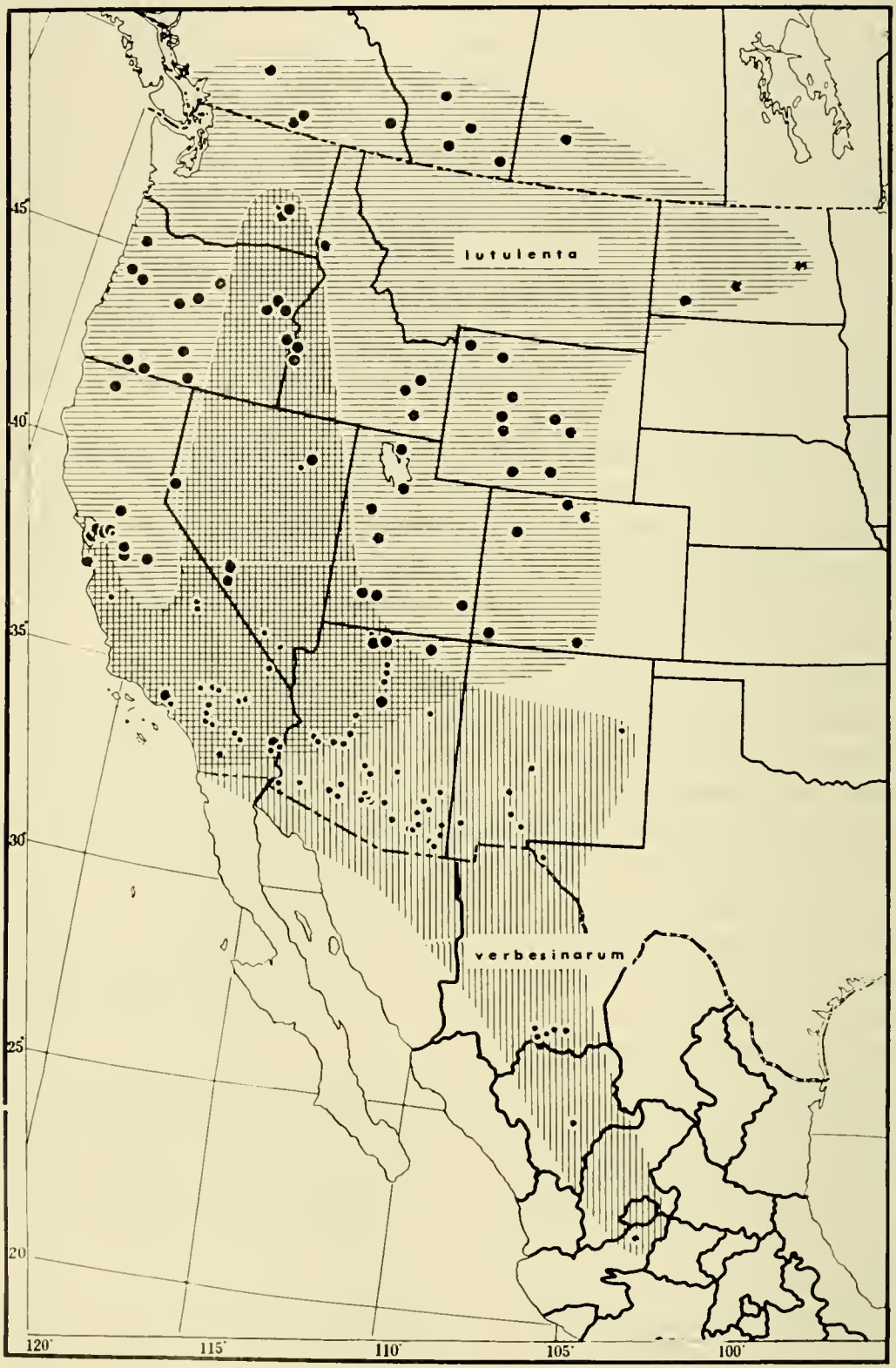


FIG. 34. Map showing the known distributions of *M. (Eumelissodes) verbesinarum* Cockerell and *M. (E.) lutulenta* LaBerge.

Picacho Pass; Prescott (32 miles S.); Red Rock; Roll; Safford; Salome (2.3 and 2.7 miles W.); San Simon; Solomon (10 miles E.); Theba; Toltec (10 miles S.); Tucson (10 miles S.); Wendel; Wenden; Wickenburg; Yuma. California: Banning; Blythe; Borego Springs; Cathedral City; Chubbock (6 miles N. E.), San Bernardino Co.; Ivanpah (8 miles S.); Joshua Tree Nat. Mon. (Pinto Basin), San Bernardino Co.; Laguna Mts., Valencio Co.; Lone Pine, Inyo Co.; Lucerne Valley; Ludlow (and 6 miles W.); Morango; Newberry; Oro Grande; Palm Springs, Pasadena; Ribbonwood; Ripley (7 miles S.); Whitney Portal, Inyo Co.; Windmill Station, San Bernardino Co. Nevada: Arden, Clark Co.; Charleston Mts., Kyle Co.; Elko. New Mexico: Buckhorn; Florida (11 miles N. E.); Garfield; Hot Springs; Isleta; Las Cruces; Lordsburg; Malaga (14 miles S.); Rodeo, San Simon Valley (10 miles N.); Socorro Tucumcari. Texas: Cornudas, Hudspeth Co.; Davis Mts.; El Paso (20 miles N.); LaTuna-Vinton Highway, El Paso Co. Washington: Lake Paha. *México.* Chihuahua: Agua Caliente, Santa Barbara District; Camargo (20 and 42 miles S. W.); Chihuahua; Parral (15 miles E.); Santa Barbara. Durango: Rodeo (12 miles N.); San Juan del Río. Jalisco: San Juan Lagos.

Flower Records. Actinea sp., *Argemone platyceros, Aster canescens, A. tenacetifolius, Baileya* sp., *B. multiradiata, Bigelovia* sp., *Cevallia sinuata, Chaenactis* sp., *Chrysothamnus* sp., *Croton californicus, Erigeron* sp., *Eysendhardtia polystachya, Geraea* sp., *G. canescens, Grindelia* sp., *Gutierrezia lucida, Helenium autumnale, Isocoma acradenia veneta, Lygodesmia juncea, Pectis papposa, Psilostrophe cooperi, Sphaeralcea* sp., *Tamarix* sp., *Verbesina encelioides.*

Melissodes (Eumelissodes) lutulenta, n. sp.

M. lutulenta is a small species extremely closely allied to *M. subagilis.* The female of *lutulenta* is difficult to separate from that of *subagilis.* The *lutulenta* female has the hairs of the anterior third of the mesoscutum erect to suberect and blunt, rather than decumbent and acute as in *subagilis.* Also, the *lutulenta* female has the pubescence of the distal pale band of tergum 2 slightly shorter than in *subagilis* as described below. The male of *lutulenta* can be readily identified by the long brown hairs medially on the scutellum and almost always posteromedially on the mesoscutum as well.

Female. Measurements and ratios: N, 20; length, 9-11 mm.; width, 3-4 mm.; wing length, $M = 2.94 \pm 0.135$ mm.; hooks in

hamulus, M = 11.80 ± 0.543; flagellar segment 1/segment 2, M = 1.89 ± 0.018.

Structure and color: Integumental color as in *subagilis*. Structure and sculpture as in *subagilis* except as follows: clypeal punctures round, regular, surface dulled at least posteriorly by coarse tessellation; lateral areas of vertex with punctures sparse; galeae tessellate above; maxillary palpal ratio about 4.0:3.0:2.5:1.0, minute fifth segment occasionally present; metasomal tergum 2 with basal area punctures separated mostly by half to one puncture width, surface shiny and unshagreened, interband zone punctures irregular in size and spacing, separated mostly by one to three puncture widths, surface shiny, reticulotransverse shagreening fine, apical area impunctate if present; tergum 3 similar to 2 but interband zone punctures more crowded; pygidial plate usually more pointed.

Hair: Head as in *subagilis* except vertex always with abundant brown. Thorax as in *subagilis* except as follows: hairs of anterior part of mesoscutum erect, blunt so that hair of dorsum has clipped appearance; dark mesoscutal and scutellar patches present, that of mesoscutum at least as large as and often twice area of scutellar patch; pale hairs white laterally to cinereous or pale orchraceous above. Metasomal vestiture as in *subagilis* except as follows: tergum 2 usually with short glabrous apical area in median two-fifths (allotype) or more and rarely across entire tergum, pale distal band always as apical area medially or more; tergum 3 often with short glabrous apical area but less than one-third width of tergum usually; tergum 2 with distal pale band white, composed of closely appressed, short, plumose hairs even near posterior margin of band; terga 5 and 6 with or without white lateral tufts; sterna dark brown, often white laterally and penultimate sternum usually white apically; posterior basitarsi with inner surfaces dark brown to black.

Male. Measurements and ratios: N, 20; length, 8-11 mm.; width 2.5-3.5 mm.; wing length, M = 11.55 ± 0.138 mm.; hooks in hamulus, M = 10.45 ± 0.135; flagellar segment 2/segment 1, M = 5.59 ± 0.121.

Structure and color: Integumental color as in *subagilis* except as follows: labrum often with mediobasal cream-colored spot (not in holotype); flagellar segment 1 usually (holotype) entirely brown; veins red to dark brown or black. Structure as in *subagilis* except as follows: minimum length first flagellar segment one-fifth to one-eighth (holotype one-sixth) maximum length second segment and more than half its own maximum length; maxillary palpal ratio

about 3.5:3.0:2.5:1.0, fifth segment rarely present. Sculpture as in female except as follows: galeae above often only delicately shagreened in less than apical half, occasionally densely shagreened and occasionally shiny; clypeal punctures smaller; tergum 1 with basal four-fifths punctate; tergum 2 with interband zone punctures slightly larger and more crowded; terga 3-5 similar to 2 but apical impunctate areas progressively shorter or absent. Terminalia as in *agilis* but sternum 8 with ventral tubercle blunt, not bidentate and gonostyli scarcely capitate.

Hair: Vestiture in general as in *subagilis* except as follows: pale hairs white to cinereous, rarely pale ochraceous; scutellum with long brown hairs medially; mesoscutum usually with abundant (as in holotype) long brown hairs posteromedially; tergum 2 often with distal pale band reaching apical margin across all (holotype) or at least lateral thirds of tergum.

Bionomics. *M. lutulenta* is an oligolege of the Compositae and seems to prefer the genera *Chrysothamnus, Grindelia* and *Solidago.*

Type Material. Holotype male, allotype female, one male and seven female paratypes were collected by F. E. Lutz at Meeker, Colorado, July 20-21, 1919. One male and seven female paratypes from Colorado are as follows: Costilla Co.: 3 females, August 10, 1934. Mesa Verde: 1 female, August 23, 1934, F. E. Lutz; 1 female, July 22, 1937, G. F. Englehardt. Glen Haven: 1 female, August 9, 1952, R. R. Dreisbach. Medicine Bow Mts.: 1 female and 1 male, August 12, 1952, R. R. Dreisbach. The holotype and allotype are in the American Museum of Natural History, New York City. Paratypes are in the collections of the American Museum of Natural History, R. R. Dreisbach of Midland, Michigan, the Snow Entomological Museum of the University of Kansas, Lawrence, and the author's collection.

Distribution. *M. lutulenta* ranges from British Columbia east to Saskatchewan and south to California, Arizona and Guanajuato in Mexico (Fig. 34). It has been collected from May 25 to October 17, but chiefly in July and August. In addition to the type material, 116 females and 77 males have been examined from the localities listed below (this list includes the type localities).

Arizona: Black Mts. (near Kayenta); Flagstaff (7 miles S.); Houserock Canyon; Jacob Lake (6 miles N.), Coconino Co. California: Antioch; Avon, Contra Costa Co.; Bear Valley, Santa Cruz Mts.; Blythe; Gazelle, Siskiyou Co.; Hopkins Well, Riverside Co.; Hospital Canyon; Juntura; Millbrae, San Mateo Co.; Modesto; Oak-

ley; Richmond; Sacramento; Turlock. COLORADO: Costillo Co.; Glen Haven; Medicine Bow Mts.; Meeker; Mesa Verde. IDAHO: Blackfoot; Downey; Homedale; Idaho Falls (Ammon Sand Hills); Lewiston; Parma. NEVADA: Deeth; Denio (50 miles S. W.), Humboldt Co.; Goldfield (and 20 miles S.); Sky Ranch, Reno. NORTH DAKOTA: Beach; Bismarck; Jamestown; Mott. OREGON: Amity (5 miles S.); Baker (10 miles S.); Bend; Corvallis; Devils Lake, Deschutte Co.; Grizzly Butte; Hereford; John Day Gorge; Klamath Falls (22 miles E.); Lakeview; Mitchell (14 miles E.); Ontario; Prineville (10 miles W.); Summer Lake; Three-Sisters. SOUTH DAKOTA: Buffalo Valley, Stanley Co. UTAH: Bear river City; Cedar Point; Dugway Proving Ground, Tooele Co.; Monticello; Panguitch; Parowan Canyon, Iron Co.; Saltair; Topaz. WASHINGTON: Lake Paha; Ritzville. WYOMING: Buffalo Bill Reservation; Carbon Co.; Lander; Owl Creek Mts.; Powder River; Rock Springs (45 miles E.); South Pass; Ten-mile Draw (E. of Casper); Yellowstone National Park. *Canada.* ALBERTA: Gleichen; Lethbridge; Medicine Hat; Scandia. BRITISH COLUMBIA: Invermeere; Kamloops; Kelowna; Nicola; Thompson River; Wasa. SASKATCHEWAN: Swift Current. *México.* GUANAJUATO: León (2 miles N. W.).

Flower Records. Achillea millefolia, Anthemis cotula, Aster spinosus, Centromadia pungens, Chaemataxis sp., *Chrysothamnus* sp., *Cleome* sp., *Grindelia* sp., *G. squarrosa, Gutierrezia* sp., *Helianthus* sp., *Melilotus alba, Solidago* sp., S. *occidentalis.*

Melissodes (Eumelissodes) utahensis, n. sp.

This small species is closely allied to *M. subagilis* and to *M. humilior.* The female of *utahensis* is like that of *subagilis* but has glabrous apical areas on terga 2 and 3 and is less densely punctate on the mesoscutum and terga. The female is like that of *humilior* but has the hairs of the inner surfaces of the hind basitarsi pale, the apical area of tergum 2 without or with very few dark hairs, and has less brown on the mesoscutum. The male of *utahensis* is similar to that of *limbus* but the dark apical hairs on the terga are usually absent and the galeae are usually shagreened above. It also closely resembles the male of *lutulenta* but is more finely punctate as described below.

Female. Measurements and ratios: N, 20; length, 9-10 mm.; width, 3.5-4.0 mm.; wing length, M = 2.98 ± 0.115 mm.; hooks in hamulus, M = 12.70 ± 0.729; flagellar segment 1/segment 2, M = 1.96 ± 0.025.

Structure and color: Integumental color as in *subagilis* except eyes gray to greenish gray. Structure and sculpture as in *subagilis* except as follows: clypeus and supraclypeal area with surfaces shiny, unshagreened or shagreening sparse and fine; lateral areas vertex with punctures minute, separated mostly by three to four puncture widths; galeae above dulled by dense reticular shagreening; maxillary palpal ratio about 4.0:3.5:3.5:1.0; mesoscutal punctures peripherally separated by half to two puncture widths, posteromedially mostly by two to three puncture widths or more, surface shiny; tergum 1 with basal three-fifths with small round punctures separated mostly by one puncture width or slightly more, apical area impunctate; tergum 2 with basal area punctures separated mostly by half to one puncture width, surface unshagreened, interband zone punctures minute, mostly smaller than those of basal area and separated mostly by two to four puncture widths, apical area impunctate; tergum 3 similar to 2 but apical area usually absent or present only in median third or less.

Hair: Head white to pale ochraceous. Thorax white laterally to ochraceous above; scutellum with brown hairs medially; mesoscutum with posteromedian patch of brown hairs no larger than scutellar dark patch and often smaller. Metasomal terga as in *subagilis* except as follows: pale distal bands of terga 2-4 white or almost white; tergum 2 with distinct glabrous apical area no longer medially than distal pale pubescent band, distal pale band usually reaching apical margin at extreme sides, interband zone hairs subappressed to suberect, white to pale ochraceous; tergum 3 with glabrous apical area often reduced to median third of tergum and shorter than in tergum 2, basal and interband zone hairs dark brown; tergum 4 similar to 3 but apical area lacking; terga 5 and 6 dark brown with pale lateral tufts. Legs as in *subagilis;* inner surfaces hind basitarsi yellow to red.

Male. Measurements and ratios: N, 16 length, about 10 mm.; width, about 3 mm.; wing length, M = 2.89 ± 0.168 mm.; hooks in hamulus, M = 10.88 ± 0.239; flagellar segment 2 /segment 1, M = 5.37 ± 0.164.

Structure and color: Integumental color as in *subagilis* except as follows: labrum often with small mediobasal cream-colored spot (especially Arizona specimens, not in allotype); flagellar segment 1 usually wholly brown or red below; wing veins reddish brown to dark brown. Structure as in *subagilis* except maxillary palpal ratio about 4:3:3:1. Sculpture as in female except as follows: tergum 1

with punctures almost to apical margin; tergum 2 with basal area with surface often (allotype) reticularly shagreened, with apical area medially as long as distal pale band or shorter; terga 3-5 similar to 2 but apical areas progressively shorter to absent. Terminalia as in *agilis* and *subagilis* (Figs. 109-110).

Hair: Head white to pale ochraceous (especially vertex). Thorax white laterally to pale ochraceous above; scutellum often with abundant brown hairs medially (especially Arizona specimens, not in allotype); mesoscutum with no (allotype) to abundant brown hairs posteromedially; tergum 1 with ochraceous hairs, near apex hairs appressed and occasionally almost obscuring marginal area; tergum 2 with basal hairs white, distal pale band white to pale ochraceous and as long as or longer than apical apubescent area medially, interband zone with suberect to erect ochraceous hairs (in Arizona specimens a few of these dark brown), apical area glabrous or with long suberect pale hairs (brown in some Arizona and Nebraska specimens); terga 3-5 similar to 2 but apical areas shorter or absent and interband and basal areas often with abundant brown hairs (not in allotype except on tergum 5); terga 6 and 7 ochraceous. Legs as in *subagilis*.

Type Material. The holotype female and nine female paratypes from Eureka, Utah, were collected by G. E. Bohart, July 20, 1949, on *Chrysothamnus* sp. The allotype male and one male paratype from Cove Fort, Utah, were collected by G. F. Knowlton, August 4, 1949. Four female and four male paratypes from Utah are as follows: Parowan, Iron Co.: 1 female, July 27, 1919. Beaver: 1 male, August 10, 1944, C. J. Sorenson. Thistle: 1 male, August 16, 1947, G. F. Knowlton. Topaz: 1 female on *Chrysothamnus* sp., August 12, 1949, Millard. Howell: 1 male, August 21, 1949, G. F. Knowlton. Tintic: 1 male, July 1951, G. F. Knowlton. Lofgreen: 1 female, July 1951, G. F. Knowlton. Dugway Proving Ground (Granite Peak) Tooele Co.: 1 female on *Chrysothamnus* sp., July 31, 1952, Loshbaugh. The holotype and allotype are in the Snow Entomological Museum of the University of Kansas, Lawrence. Paratypes are in the collections of the Snow Entomological Museum, Utah State University, Logan, the University of Utah, Salt Lake City, and in the author's collection.

Distribution. M. utahensis is known only from Utah, Arizona, Southern California and Nebraska (Fig. 35). It has been collected from July 20 to September 28. In addition to the type ma-

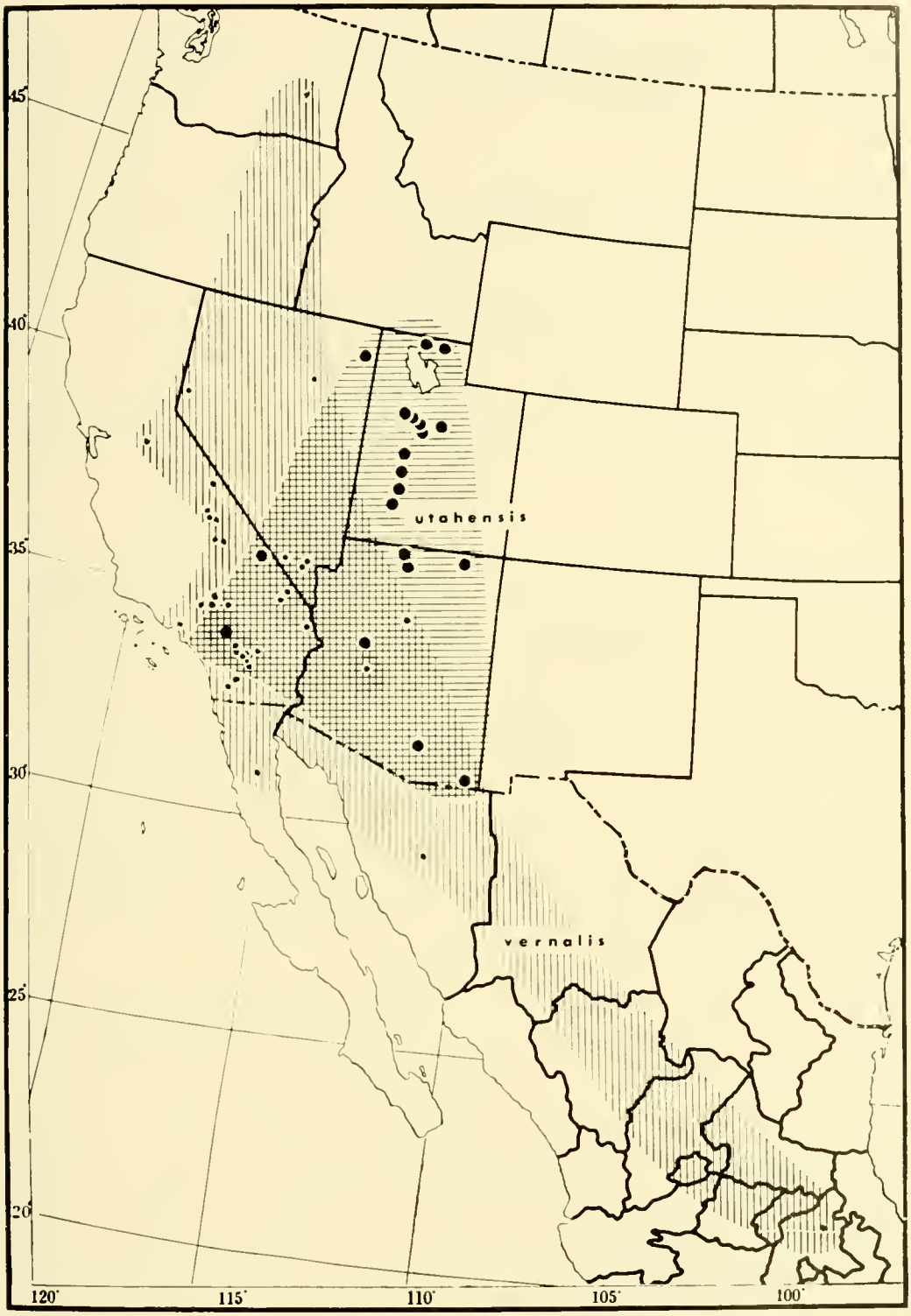


FIG. 35. Map showing the known distributions of *M. (Eumelissodes) vernalis* LaBerge and *M. (E.) utahensis* LaBerge.

terial listed above, 11 females and 5 males have been examined. The data for these is given below in full.

ARIZONA: Black Mesa (near Kayenta): 2 females on *Chaemataxis* sp., September 11, 1938, I. McCracken. Douglas: 1 male, August

20, 1933, W. W. Jones. Grand Canyon: 6 females and 1 male, August 19, 1939, E. C. Van Dyke; 2 males, July 26, 1954, H. E. and M. A. Evans. Jacob Lake, Coconino Co.: 1 male, July 24, 1952, Cazier, Gertsch and Schrammel. Kirkland (Peeples Valley), Yavapai Co.: 1 female, August 22-24, 1927. Sabino Basin, Santa Catalina Mts.: 2 females, September 28, C. H. T. Townsend. CALIFORNIA: Santa Ana River, San Bernardino Co.: 1 female on *Gutierrezia californica*, 1 male on *Chrysothamnus nauseosum*, August 23, 1952, P. H. Timberlake; Westgard Pass, Inyo Co.: 1 male, July 10, 1953, E. G. Linsley. NEBRASKA: Monroe Canyon, Sioux Co.; 1 male, August 18, 1912, E. J. Taylor. NEVADA: Oasis (20 miles W.): 1 female, August 12, 1951, A. T. McClay. UTAH: Cache Junction.

Melissodes (*Eumelissodes*) *brevipyga*, n. sp.

This small desert bee is closely related to *M. verbesinarum* and the females of the two species are very similar. The *brevipyga* female has smaller eyes (not twice or more as broad as the gular area in profile as in *verbesinarum*), the apical area of tergum 2 (and usually of tergum 3) glabrous, and vein 2nd m-cu interstitial with vein 2nd r-m in the fore wing. The female of *brevipyga* also resembles that of *humilior* and that of *utahensis* but can be separated from these by the shiny galeae, as well as the venation character given above. The male of *brevipyga* has a distinctive short broad pygidial plate, shiny galeae, black mandibular bases, and a conspicuous white mediobasal labral macula.

Female. Measurements and ratios: N, 20, length 8-11 mm.; width, 3-4 mm.; wing length, $M = 2.93 \pm 0.058$ mm.; hooks in hamulus, $M = 11.95 \pm 0.135$; flagellar segment 1/segment 2, $M = 1.83 \pm 0.018$.

Structure and color: Integumental color as in *subagilis*. Structure and sculpture as in *subagilis* except as follows: clypeal punctures crowded, surface shiny, unshagreened, apicomedian carina usually reduced to a small subapical boss; lateral areas of vertex with small shallow punctures separated by one to three puncture widths, often dulled by fine tessellation (as in allotype); galeae shiny, unshagreened above except in apical one half or less; maxillary palpal ratio about 14:8:6:1, fourth segment often completely lacking, second and third usually seem to be fused; mesoscutal punctures large, deep, posteromedian area impunctate or with scattered large punctures; fore wings with vein 2nd m-cu interstitial with vein 2nd r-m; tergum 1 with basal area punctures separated mostly by half a

puncture width or less, surface shiny, interband zone punctures distinct, separated by half to one puncture width, apical area impunctate, shiny; tergum 3 similar to 2 but interband zone punctures more crowded; pygidial plate no longer than broad at base, apex well rounded.

Hair: Head white. Thorax white, scutellum occasionally with several brown medially, mesoscutum occasionally with sparse brown posteromedially. Tergum 1 with long white basally, with short white appressed pubescence near apical margin in lateral fifths or less; tergum 2 white basally, distal pale band white, about as long medially as apical area, uninterrupted, interband zone hairs short, appressed to suberect, white, apical area bare; tergum 3 similar to 2 but basal tomentum and interband zone hairs dark brown and apical area shorter; tergum 4 similar to 3 but distal pale band apical; terga 5 and 6 dark brown medially to white laterally. Legs white except as follows: fore tarsi pale brown; outer-apical surfaces middle tibiae pale brown; basitibial plates brown; inner surfaces hind basitarsi dark brown to reddish brown (allotype).

Male. Measurements and ratios: N, 20; length, 9-10 mm.; width, 2-3 mm.; wing length, $M = 2.69 \pm 0.123$ mm.; hooks in hamulus, $M = 11.15 \pm 0.131$; flagellar segment 2 segment 1, $M = 6.07 \pm 0.064$.

Structure and color: Integumental color as in *subagilis* except as follows: clypeus pale yellow; labrum with large mediobasal white spot equaling more than one-third area of labrum; mandibles without basal yellow spots. Structure as in *subagilis* except as follows: minimum length first flagellar segment one-sixth to one-eighth maximum length second segment; maxillary palpal ratio about 4.0:2.7:2.0:1.0, fourth segment much shorter or virtually absent in some specimens; pygidial plate short and broad, usually broader at base than median length. Sculpture as in female except as follows: mesoscutal punctures more crowded, especially posteromedially; tergum 1 with basal four-fifths punctate; tergum 2 with interband zone punctures often separated by one to two puncture widths; terga 3-5 similar to 2 but interband zone punctures more crowded and apical areas progressively shorter to absent. Terminalia as in *agilis* and *subagilis* (Figs. 111-112).

Hair: Head white. Thorax white, on mesoscutum especially, and usually on scutellum, long white hairs decumbent. Metasomal vestiture as in *subagilis* except generally white. Legs as in *subagilis* but white.

Bionomics. *M. brevipyga* seems to be restricted to the desert regions of the southwest. It is an oligolege of the Compositae and seems to prefer the genera *Isocoma* and *Aster* in that order, and has been collected mostly from these two genera.

Type Material. The holotype male, allotype female, and two male and fourteen female paratypes were collected seven miles south of Ripley, Riverside Co., California, October 19, 1951, on *Aster* sp., by P. D. Hurd. In addition, 55 female and 7 male paratypes were collected seven miles south of Ripley, California, October 19, 1951, by P. H. Timberlake as follows: 2 females on *Baccharis* sp., 48 females and 4 males on *Aster tephrodes*, 1 female on *Aster spinosus*, and 4 females and 3 males on *Palofoxia linearis*. The holotype and allotype are in the collection of the University of California at Berkeley. Paratypes are in the collections of the University of California, Prof. P. H. Timberlake, Citrus Experiment Station, Riverside, California, the Snow Entomological Museum of the University of Kansas, Lawrence, and in the author's collection.

Distribution. *M. brevipyga* is known from California, Arizona and Idaho (Fig. 32). It has been collected from June 26 to November 15, but chiefly in October. In addition to the type material, 136 females and 13 males have been examined from localities listed below (the list includes the type locality).

ARIZONA: Two-gun, Coconino Co.; Yuma. CALIFORNIA: Coachella, Riverside Co.; Deep Springs, Inyo Co.; Helendale, Mojave Desert; Hopkins Well, Riverside Co.; Indio (and 2.8 miles S. E. and 6 miles N. W.); Newberry, San Bernardino Co.; Piñon Flat; Ripley (7 miles S.); San Diego; Westgard Pass (3 miles N.), Inyo Co. IDAHO: Declo.

Flower Records. *Aster* sp., *A. spinulosus*, *A. tephrodes*, *Baccharis* sp., *Chrysothamnus* sp., *Gutierrezia californica*, *G. sarothrae*, *Isocoma* sp., *I. acradenia*, *Palofoxia linearis*.

Melissodes (Eumelissodes) vernalis, n. sp.

This small species is closely related to *M. limbus*. The female of *vernalis* is similar to that of *limbus* but has shiny galeae, less punctate mesoscutum, and the tergal apices translucent, usually smoky to almost colorless. The male is like that of *limbus* except the galeae are shiny above and the pygidial plate is narrower than usual for a *Eumelissodes* species.

Female. Measurements and ratios: N, 20; length, 9-12 mm.;

width, 3.5-4.0 mm.; wing length, M = 3.00 ± 0.123 mm.; hooks in hamulus, M = 12.30 ± 0.179; flagellar segment 1/segment 2, M = 1.82 ± 0.066.

Structure and color: Integumental color as in *subagilis* except as follows: eyes gray to bright green (holotype); wing veins dark brown to black; tegulae not usually rufescent, piceous, tergum 1 with broad hyaline, red to colorless margin (red in holotype); terga 2-4 with apical areas translucent and smoky to hyaline and colorless.

Structure and sculpture as in *subagilis* except as follows: clypeal surface unshagreened; supraclypeal area usually with abundant punctures, surface shiny; lateral areas vertex with minute punctures separated by two to four puncture widths, surface shiny; galeae shiny above, unshagreened except near tips; maxillary palpal ratio about 4.0:3.0:2.5:1.0; mesoscutum with posteromedian area impunctate or with scattered punctures, mesoscutal punctures smaller than in *brevipyga;* metasomal tergum 1 with basal half with small shallow punctures separated mostly by one puncture width, surface and bottoms of punctures dulled by shagreening, apical area with distinct anterolateral impunctate lobes; tergum 2 with basal area punctures separated mostly by one puncture width, surface shiny, interband zone punctures minute, smaller than those of basal area, separated mostly by two to four puncture widths, apical area impunctate; tergum 3 similar to 2 but apical area lacking or restricted to one-third or less of width of tergum (less in holotype) and shorter; tergum 4 similar to 3 but lacking apical area; pygidial plate as in *subagilis.*

Hair: Head white except long brown on vertex. Thorax white laterally, pale ochraceous to white dorsally except abundant brown on scutellum and mesoscutum, mesoscutal dark patch as large as to twice size of scutellar (in holotype twice size); tegulae often with brown (present in holotype). Tergum 1 with long white hairs basally, glabrous apically, anterolateral lobes of apical area often with minute, simple, closely appressed, brown hairs (holotype); tergum 2 white basally, distal pale band white, interband zone about as long medially as distal pale band and with short, appressed to suberect, dark brown hairs, apical area with abundant suberect dark brown hairs; tergum 3 similar to 2 but basal tomentum brown and apical area shorter, not as wide and occasionally absent; tergum 4 similar to 3 but apical area absent; terga 5 and 6 pale brown medially (often darker basally) with white lateral

tufts; sterna yellow to reddish brown medially, white laterally and apically. Legs as in *limbus*.

Male. Measurements and ratios: N, 20; length, 9-11 mm.; width, 2.5-3.5 mm.; wing length, M = 2.90 ± 0.114 mm.; hooks in hamulus, M = 11.60 ± 0.775; flagellar segment 2/segment 1, M = 6.03 ± 0.127.

Structure and color: Integumental color as in *subagilis* except as follows: labrum with large mediobasal white or cream-colored spot equal to more than one-third and often more than one-half area of labrum; wing veins dark reddish brown to black.

Structure as in *subagilis* except as follows: minimum length first flagellar segment equals one-sixth to one-eighth maximum length second segment; maxillary palpal ratio about 3.5:3.0:2.5:1.0; pygidial plate long and narrow, usually about twice as long as median width, with weakly defined apicolateral notches. Sculpture as in female except as follows: clypeal punctures weak; tergum 1 punctate to within one-sixth or one-fifth of apical margin; terga 2 and 3 with interband zones with small round distinct punctures separated mostly by two to three puncture widths; terga 4 and 5 similar to 2 but apical areas shorter or absent. Terminalia as in *agilis* but sternum 8 with ventral tubercle acute, not bidentate (Figs. 113-114).

Hair: Head white. Thorax white except scutellum brown medially and mesoscutum usually with posteromedian brown patch as large as or slightly larger than scutellar dark patch. Metasomal vestiture as in *subagilis* except as follows: generally white rather than ochraceous; tergum 2 with distal pale band usually as long as or slightly shorter than apical apubescent area medially. Legs as in *subagilis* but white.

Bionomics. *M. vernalis* is another composite oligolege and seems to prefer the genera *Encelia* and *Geraea* to all others. However, the available floral data are very scant.

Type Material. The holotype female with one female paratype from Mazourka Canyon, Inyo Mts., Inyo Co., California, was collected by C. D. Michener, June 1, 1937, on *Encelia farinosa*. The allotype male from the same locality and flower was collected by C. D. Michener on June 11, 1937. In addition, 15 females and 14 male paratypes from Inyo Co., California, are as follows: Mazourka Canyon: 1 female, May 25, 1937, N. W. Frazier. Inyo Mts.: 1 male, May 23, 1937; 1 male, June 1, 1937, E. C. Van Dyke; 1 male,

June 5, 1939, on *Sphaeralcea ambigua*, R. M. Bohart. Lone Pine: 1 male, May 19, 1937, 2 males, June 9, 1937, E. C. Van Dyke. Panamint Mts.: 1 male, May 24, 1937, W. C. Reeves; 11 females and 3 males, May 30, 1937, E. C. Van Dyke. Argus Mts. (near Darwin Falls): 1 female, May 30, 1937, C. D. Michener. Keeler (4 miles S. E.): 1 male, May 22, 1937, on *S. ambigua*, E. C. Van Dyke; 1 male, May 22, 1937, on *S. ambigua*, C. D. Michener; Westgard Pass: 2 females (7 miles W.), June 26, 1953, J. W. MacSwain; 2 males, June 13, 1937, G. E. Bohart. The holotypes and allotype are in the Snow Entomological Museum of the University of Kansas, Lawrence. Paratypes are in the collections of the Snow Entomological Museum, the California Academy of Sciences, San Francisco, the American Museum of Natural History, New York City, the University of California, Berkeley, the Utah State University, Logan, and in the author's collection.

Distribution. M. vernalis ranges from Washington south to Baja California and Hidalgo in Mexico, and east to Nevada (Fig. 35). It has been collected from March 28 to October 12, but mainly in April, May and June. In addition to the type material, 60 females and 60 males have been examined from the localities listed below (list includes type localities).

Arizona: Oak Creek Canyon; Wellton; Wickenburg (20 miles N. W.). California: Andreas Canyon; Argus Mts. (near Darwin Falls); Beal Well; Bonanza Mine, Providence Mts.; Borego; Box Canyon, Riverside Co.; Cathedral City; Edom, Riverside Co.; Fish Springs; Indio; Inyo Mts.; Kane Spring (7, 8 miles N. W.); Keeler (4 miles S. E.); Kramer; Lone Pine; Los Angeles; Los Angeles Co.; Lovejoy Buttes; Mazourka Canyon, Inyo Mts.; Mecca (3 miles S.), Riverside Co.; Micheli Caverns, San Bernardino Co.; Mojave Desert; New York Mts.; Oasis, Mono Co.; Palm Canyon; Palm Springs, Panamint Mts.; San Diego Co.; Snow Creek, San Jacinto Mts.; Thousand Palms; Valley Spring (3 miles E.); Westgard Pass (7 miles W.); Yermo, San Bernardino Co. Nevada: Arden (3 miles E.); Charleston Mts., Clark Co.; Las Vegas; Lee Canyon; Reno (29 miles E.). Washington: Ritzville. *México.* Baja California: San Augustine. Hidalgo: Pachuca. Sonora: San Bernardo.

Flower Records. Aster abatus, A. agnatus, Baileya sp., *B. multiradiata, Bebbia juncea, Chilopsis linearis, Encelia* sp., *E. farinosa, Geraea* sp., *G. canescens, Hyptis emoryi, Melilotus* sp., *Prosopis* sp., *Psilostrophe cooperi, Sphaeralcea ambigua, Viguiera deltoides.*

Melissodes (Eumelissodes) velutina (Cockerell)

Exomalposis velutinus Cockerell, 1916, Pomona Jour. Ent. Zool., vol 8, p. 58; Bray, 1917, Pomona Jour. Ent. Zool., vol. 9, p. 95.
Melissodes velutina, Michener, 1951, *in* Muesebeck *et al,* Hymenoptera of America North of Mexico, Synoptic Catalog, U. S. Dept. Agric., Agric. Monogr. No. 2, p. 1229.

Melissodes velutina is a distinctive pale bee from the deserts of southern California. It is closely related to *M. vernalis.* The female is distinctive in having translucent, smoky or rufescent, tergal apices, pale hairs on terga 5 and 6, and somewhat infumate wing membranes. The male is like that of *verbesinarum* in having both a large mediobasal pale labral spot and large yellow basal mandibular spots, but differs in that the wings are somewhat infumate, the wing veins are dark brown to black, and the pygidial plate quite narrow.

Female. Measurements and ratios: N, 20; length, 9-12 mm.; width, 3-4 mm.; wing length, M = 2.80 ± 0.149 mm.; hooks in hamulus, M = 12.85 ± 0.997; flagellar segment 1/segment 2, M = 1.87 ± 0.022.

Structure and color: Integumental color as in *subagilis* except as follows: tergum 1 with apical third rufescent to yellow; terga 2-4 with apical areas translucent, yellow to smoky red (usually deeper color basad); eyes gray to bluish gray; wing membranes somewhat infumate, yellowish brown, veins dark brown to black; tegulae piceous.

Structure and sculpture as in *subagilis* except as follows: clypeal punctures coarse, separated mostly by less than half a puncture width, surface shiny, bottoms of punctures tessellate (at least larger punctures), mediobasal carina weakly developed; supraclypeal area punctate, unshagreened; galeae above unshagreened; lateral areas vertex with punctures separated mostly by one to two puncture widths, surface shiny; maxillary palpal ratio about 2.7:2.7:2.5:1.0; posteromedial mesoscutal area with scattered punctures separated mostly by one to three puncture widths; metasomal tergum 1 with basal three-fifths punctate; tergum 2 with basal area punctures minute, separated mostly by two or more puncture widths, interband zone punctures slightly larger, separated mostly by two to three puncture widths, apical area impunctate; tergum 3 similar to 2 but apical area absent or reduced to apicomedian triangle; pygidial plate V-shaped, rounded apically, longer than broad.

Hair: Head white to ochraceous with scattered brown hairs on vertex. Thorax white or pale ochraceous laterally, ochraceous to

yellow above except scutellum dark brown with pale fringe, mesoscutum with posteromedian dark brown patch about twice size of scutellar dark area, and tegulae dark brown. Metasomal tergum 1 pale ochraceous basally, anterolateral lobes of apical area with short, subappressed, dark brown hairs, with white to pale ochraceous, appressed pubescence apical to anterolateral lobes; tergum 2 white basally, distal pale band white to pale ochraceous, reaching apical margin at extreme sides, narrowly connected to basal white band at extreme sides, longer than apical area medially; interband zone with short, subappressed, dark brown hairs, apical area with short, suberect, ochraceous to brown hairs; tergum 3 similar to 2 but distal pale band reaching apical margin across all or most of tergum, apical area, if present, reduced to small triangular or diamond-shaped area usually less than one-third width of tergum, interband zone with scattered short white pubescence; tergum 4 like 3 but apical area absent; terga 5 and 6 ochraceous to orange medially to white laterally (darker basally); sterna orange to brown with white apical fringes. Legs white except as follows: fore tarsi pale brown; outer-apical surfaces fore and middle tarsi orange to pale brown; basitibial plates orange-brown; inner surfaces hind basitarsi yellow to orange-red.

Male. Measurements and ratios: N, 20; length, 9-11 mm.; width, 2.5-3.5 mm.; wing length, M = 2.73 ± 0.133 mm.; hooks in hamulus, M = 11.00 ± 0.670; flagellar segment 2/segment 1, M = 6.83 ± 0.183.

Structure and color: Integumental color as in *subagilis* except as follows: labrum cream-colored to white with brown apical margin; mandibles with large basal yellow spots; eyes gray to bluish gray; wing membranes slightly infumate, veins dark brown; tegulae piceous; tergal apices translucent, colorless to yellowish brown.

Structure as in *subagilis* except as follows: minimum length first segment about one-sixth maximum length second segment, minimum width penultimate segment slightly less than one-third length, flagellum reaches slightly beyond pterostigma in repose; maxillary palpal ratio about 3.5:2.5:2.5:1.0; pygidial plate narrow, almost twice as long as median width, subapical notches indistinct. Sculpture as in female except as follows: mesoscutum often impunctate posteromedially; tergum 1 with basal four-fifths punctate; terga 3-5 similar to 2 but apical areas progressively shorter; terga 2-4 with interband zone punctures larger and more abundant. Terminalia much as in *agilis;* gonostyli narrow and long; sternum 7

with median plate extending apically and outward viewed from posterior edge it is boot-shaped or shoe-shaped; sternum 8 with ventral tubercle large, blunt, not bidentate.

Hair: Head and thorax white to pale ochraceous but scutellum with dark brown medially and mesoscutum with dark brown posteromedian patch usually present and rarely larger than scutellar dark areas and never twice as large. Metasomal vestiture as in *subagilis* except as follows: tergum 1 with subappressed apical hairs often dark brown or brown, usually white; tergum 2 with interband zone and apical area hairs usually white, often brown to dark brown; terga 3 and 4 often with brown suberect hairs apically, interband zones often with some erect brown bristlelike hairs. Legs as in *subagilis*.

Bionomics. *M. velutina* seems to be an oligolege of the genus *Hugelia* (Polemoniaceae). Out of a total of 79 collections (117 females and 9 males) bearing floral data, 42 collections (82 females and 2 males) were made from some species of *Hugelia* (mostly *H. virgata*). It has also been collected on a number of composites among which *Gutierrezia* was the most often visited (10 collections of 11 females). Among the other families of plants from which *velutina* has been collected only the Boraginaceae appears important. (*Cryptantha intermedia* with five collections of five females and one male.)

Type Material. The holotype female of *velutina* from Claremont, California, collected by Baker, is in the collection of the American Museum of Natural History, New York City.

Distribution. *M. velutina* is known only from southern California north to Antioch (Fig. 33). It has been collected from April 3 to August 11 but chiefly in May and June. In addition to the holotype, 152 females and 37 males have been examined from the localities listed below.

CALIFORNIA: Aguanga; Alpine; Altadena; Andreas Canyon, Inyo Co.; Antioch; Banning; Bonanza Mine, Providence Mts.; Cabazon, Riverside Co.; Cajon Pass, San Bernardino Co.; Cajon Valley; Claremont; Coalinga (4 miles W.); Colton; Contra Costa Co.; Corona; Crestline, San Bernardino Co.; Devore (and 3 miles S. W.); Eagle Rock Hills, Los Angeles Co.; Gavilan; Gillman Hot Springs, Riverside Co.; Imperial Co.; Kern Camp (8 miles W.), San Jacinto Mts.; Los Angeles Co.; Lovejoy Buttes; Ontario; Palm Springs; Panamint Mts., Inyo Co.; Pasadena; Perris (1.5 miles W.); Phelan; Pocatello Island; Riverside; San Bernardino; San Felipe Creek; San Gabriel

Mts. (near Pasadena); Sequoia National Park (Ash Mt.); Tanbark Flat, Los Angeles Co.; Watts Valley, Fresno Co.; Yankee Hill, Butte Co.

Flower Records. Acanthopappus sphaerocephalus, Aster abatus, Chorizantha statioloides, Cirsium sp., *Coreopsis* sp., *C. lanceolatum, Cryptantha intermedia, Eremocarpus setiger, Eriogonum fasciculatum, Gutierrezia californica, G. sarothrae, Helianthus gracilentus, Heliotropium oculatum, Hugelia ambigua, H. virgata, Lotus scoparius, Marrubium vulgare, Mirabilis laevis, Monarda lanceolata, Prosopis* sp., *Salvia columbaris, Trichostema lanatum.*

Melissodes (Eumelissodes) saponellus Cockerell

Melissodes saponellus Cockerell, 1908, Canadian Ent., vol. 40, p. 234.

This small species is known only in the female sex. It is clearly related to *M. velutina* and resembles the latter in the translucent tergal apices which are in *saponellus* colorless or very nearly so. The female of *saponellus* differs from that of *velutina* by the small impunctate posteromedian area of the mesoscutum, the colorless to slightly milky wing membranes and paler veins, the lack of brown hairs on mesoscutum, scutellum and tegulae, and the slightly different punctation of the second tergum as described below.

Female. Measurements and ratios: N, 17; length, 10-11 mm.; width, 3.5-4.0 mm.; wing length, M = 2.97 ± 0.088 mm.; hooks in hamulus, M = 11.71 ± 0.187; flagellar segment 1/segment 2, M = 1.85 ± 0.023.

Structure and color: Integumental color as in *velutina* except as follows: apical areas terga 2-4 colorless to extremely slightly yellowish, tergum 1 broadly hyaline and colorless apically, hyaline area becoming yellow to red basad; eyes gray to yellowish or greenish gray; wing membranes not infumate, colorless or slightly milky, veins dark red to reddish brown; tegulae usually rufescent. Structure and sculpture as in *velutina* except as follows: clypeal punctures slightly smaller especially apically; maxillary palpal ratio about 8:5:4:1; mesoscutum with posteromedian area impunctate or with scattered punctures separated by less than half to five or more puncture widths; tergum 1 with basal three-fifths with punctures separated mostly by half to one puncture width; tergum 2 with basal area punctures larger, separated mostly by half a puncture width, surface dulled by fine reticular shagreening, interband zone punctures of similar size, irregular, spaced by half to three puncture widths; pygidial plate broadly rounded, almost U-shaped.

Hair: Head and thorax white, without brown on vertex, tegulae, mesoscutum, or scutellum. Metasomal vestiture as in *velutina* except as follows: entirely white except terga 4 and 5 ochraceous mediobasally; tergum 2 with distal pale band reaching apex laterally and twice as long as apical area medially; tergum 3 with apical area absent or reduced to extremely short area about one-fourth width of tergum; sterna yellow except white apical fringe on each and white laterally. Legs white except as follows: fore tarsi ochraceous; outer-apical surface middle and often fore tibiae pale orange; basitibial plates orange; inner surfaces hind basitarsi yellow to orange-red.

Type Material. The holotype female from Grand Coulee (Soap Lake), Washington, collected on June 29, 1902, is in the collection of Prof. P. H. Timberlake of the Citrus Experiment Station, Riverside, California.

Distribution. M. saponellus is known from the states of Washington, Oregon, Utah, and Colorado (Fig. 29). In addition to the holotype, 17 females have been examined. Data for these is given in full below.

COLORADO: Delta (5 miles N.): 1 female, June 30, 1938, U. Lanham. OREGON: Powell Butte, Crook Co.: 1 female on Alsike clover, July 11, 1941, H. A. Scullen. UTAH: Bluff: 1 female, July 7, 1935, C. Brues. Jensen (12 miles E.): 3 females on *Sphaeralcea* sp., P. H. Timberlake. Oak City: 1 female, June 24, 1949, G. E. Bohart. Vernal (5 miles N.): 7 females on *Chaenactis stenioides* and 1 female on *Bahia oblongifolia*, June 24, 1950, C. D. Michener. Zion Canyon: 2 females, May 6, 1948, G. E. Bohart. WASHINGTON: Grand Coulee (Soap Lake): holotype female.

Melissodes (Eumelissodes) appressa, n. sp.

M. appressa is a small species known only from California and related to *M. subagilis*. The female is distinctive in the form of the distal pubescent band of tergum 2 and of the pubescence composing that band as described below. The female also has the hairs of the mesoscutum short, blunt-tipped, and decumbent, as in certain members of the *microsticta* group, shiny galeae, and dark reddish brown hairs on the inner surfaces of the hind basitarsi. The male of *appressa* is like that of *subagilis* in the antennal lengths and color of the labrum and mandible, but is more like the male of *verbesinarum* in the tergal vestiture and in the shiny galeae.

Female. Measurements and ratios: N, 20; length, 10-12 mm.; width, 3-4 mm.; wing length, M = 2.67 ± 0.153 mm.; hooks in hamulus, M = 12.45 ± 0.153; flagellar segment 1/segment 2, M = 1.98 ± 0.017.

Structure and color: Integumental color as in *subagilis* except as follows: tergal apices only slightly rufescent; wing veins dark reddish brown; tegulae piceous.

Structure and sculpture as in *subagilis* except as follows: clypeal punctures large, separated mostly by half puncture width or less, surface shiny, apicomedian carina weak; galeae above shiny, unshagreened except in apical third or less; maxillary palpal ratio about 2.7:2.0:1.7:1.0; third flagellar segment with length subequal to maximum width; mesoscutum with posteromedian area punctures large, separated mostly by one to two puncture widths except in small posteromedial impunctate area usually present, peripherally punctures separated mostly by half to one puncture width, surface shiny; metasomal tergum 1 with basal three-fifths with punctures separated mostly by half to one puncture width or slightly more, apical area impunctate, shiny, without impunctate anterolateral lobes; tergum 2 with basal area punctures separated mostly by one puncture width, surface shiny but may have fine reticular shagreening, interband zone punctures slightly larger than basal area punctures, regularly spaced, separated mostly by one puncture width or slightly more, apical area, if present, impunctate, but small punctures present beneath pubescence of distal pale band; terga 3 and 4 like 2 but interband zone punctures denser and apical areas usually lacking; pygidial plate V-shaped, apex rounded.

Hair: Head white to pale ochraceous with abundant brown on vertex. Thorax white to pale ochraceous laterally; mesoscutum pale ochraceous to yellowish with large posteromedian dark brown patch usually about twice size of scutellar dark area, occasionally larger; mesoscutal hairs blunt-tipped giving clipped appearance, decumbent in anterior third. Metasomal tergum 1 white to pale ochraceous basally and to apical margin at sides, apicomedially glabrous; tergum 2 with basal white tomentum connected at extreme sides with distal white to pale ochraceous band, distal pale band reaches apical margin at least in lateral fifths and often across most of tergum, composed of short, broad, scalelike, appressed pubescence which in apical half of band (especially medially) do not or barely overlap one another, each hair twice as long as broad or shorter, occasionally along apical margin of band and especially medially

some pubescence brown, apical area when present bare or with one or two irregular rows of short, brown, appressed to subappressed, simple hairs; tergum 3 like 2 but basal tomentum brown, apical area usually absent or extremely short and no broader than one-third width of tergum, and short, pale, appressed pubescence of distal band also covers interband zone, but hairs longer; tergum 4 like 3 but apical area absent; terga 5 and 6 dark brown with white lateral tufts; sterna yellow medially, white apically and laterally on each but the last. Legs as in *subagilis* but scopal hairs white and inner surfaces hind basitarsi dark reddish brown to red.

Male. Measurements and ratios: N, 20; length, 8-11 mm.; width, 2.5-3.0 mm.; wing length, $M = 2.56 \pm 0.144$ mm.; hooks in hamulus, $M = 11.40 \pm 0.152$; flagellar segment 2/segment 1, $M = 5.86 \pm 0.145$.

Structure and color: Integumental color as in *subagilis* except as follows: wing veins red to reddish brown; tergal apices colorless.

Structure as in *subagilis* except as follows: minimum length first flagellar segment usually one-seventh to one-eighth maximum length second segment, flagellum in repose reaching or slightly surpassing pterostigma, penultimate segment more than three times as long as broad; maxillary palpal ratio about 3.0:2.5:2.0:1.0; sternum 6 with subapical oblique carinae weakly developed. Sculpture as in female except as follows: mesoscutum often without impunctate posteromedian area; metasomal tergum 1 punctate almost to apical margin; terga 2 to 4 with interband zones with punctures sparser, separated by one to two puncture widths, apical areas usually lacking.

Hair: Head and thorax white, occasionally pale ochraceous on mesoscutum; mesoscutal hairs not blunt-tipped, often decumbent in apical third. Metasomal tergum 1 with white to pale ochraceous hairs, in apical fifth to fourth hairs appressed and forming apical band obscuring apical margin of tergum; tergum 2 with white basal tomentum, white distal pubescent band which reaches apical margin in lateral fourths or more, occasionally reaching apex across entire tergum, apical area when present less than half length of distal pale band medially, half or less width of tergum, and glabrous, interband zone with long, suberect to erect, pale hairs; terga 3-5 similar to 2 but distal pale band apical (or tergum 3 occasionally with small glabrous apical area); terga 6 and 7 ochraceous to white; sterna yellow medially to white laterally. Legs white except inner surfaces tarsi yellow. Terminalia as in *agilis* and *subagilis*.

Bionomics. *M. appressa* is an oligolege of the Compositae. It seems to prefer the genera *Isocoma*, *Gutierrezia*, and *Heterotheca* in that order. The available floral data are summarized in Table XVII. Most of these data are due to the assiduous collecting of Prof. P. H. Timberlake in the Riverside area of southern California.

Type Material. The holotype female collected at Riverside, California, September 25, 1927, on *Isocoma vernonioides* by P. H. Timberlake. The allotype male and seventeen female paratypes were collected by Timberlake at Riverside on *I. vernonioides* on September 18, 1927. In addition to these, 14 female and 9 male paratypes were collected by P. H. Timberlake at Riverside, California, during 1927, as follows: 2 females, 1 male, on *I. vernonioides*, September 11; 1 male on *Gutierrezia sarothrae*, September 12; 1 female on *G. sarothrae*, September 19; 1 female on *I. vernonioides*, September 20; 1 female on *Heterotheca grandiflora*, September 27; 2 females and 1 male on *I. vernonioides*, September 29; 2 females and 2 males on *I. vernonioides* October 2; 2 females and 1 male on *I. vernonioides*, October 9; 1 female on *H. grandiflora*, October 10; 1 male on *G. sarothrae*, October 13; 1 female on *I. vernonioides*, October 15; 1 female and 1 male on *I. vernonioides*, October 16; 1 male on *Ericameria palmeri*, October 18. The holotype and allotype are in the collection of Prof. P. H. Timberlake of the Citrus

TABLE XVII. Summary of Flower Records for *Melissodes appressa*.

Plant Data			Records of *M. appressa*			
FAMILY	Number of genera	Number of species	Number of collections	Number of females	Number of males	Total number of bees
Compositae: *Isocoma* spp.	1	2	48	107	33	140
Gutierrezia spp.	1	3	54	58	29	87
Heterotheca sp.	1	1	20	22	5	27
Other genera	10	11	23	19	40	59
Other families (3)	3	3	3	0	3	3
Totals	16	20	148	206	110	316

Experiment Station, Riverside, California. Paratypes are in the collections of P. H. Timberlake, The California Academy of Sciences, San Francisco, the U. S. National Museum, Washington, D. C., the Snow Entomological Museum of the University of Kansas, Lawrence, and in the author's collection.

Distribution. *M. appressa* is known only from California (Fig. 29). It has been collected from August 14 to November 10, but chiefly in September and October. In addition to the type material, 187 females and 117 males have been studied from the localities listed below.

CALIFORNIA: Altadena; Anaheim; Antioch; Benicia; Blythe; Cortago; Cushinberry Springs; Davis; Dos Palos; Elkhorn Ferry, Yolo Co.; Firebaugh; Gazelle; Highland (E. of), San Bernardino Co.; Inyo Mts., Inyo Co.; Ivanpah, San Bernardino Co.; Los Angeles Co.; McCloud, Siskiyou Co.; Millbrae; Morongo Valley; Riverside; Sacramento; Santa Ana River (near Yorba Linda); Sierraville; Standish (4 miles W.); Turlock; Victorville; Vina, Tehama Co.

Flower Records. *Alyssum maritinum, Aster* sp., *A. exilis, Centromadia pungens, Croton californica, Ericameria palmeri, Grindelia californica, Gutierrezia californica, G. lucida, G. sarothrae, Helianthus annuus, Heliotropium oculatum, Heterotheca grandiflora, Isocoma acradenia, I. vernonioides, Lessingia glandulifera, Melilotus alba, Pluchea camphorata, Senecio sp., Solidago anfinis, S. occidentalis.*

Melissodes (Eumelissodes) pullatella, n. sp.

This is a small dark species from Oregon known only in the female sex. *M. pullatella* seems to be closely related to *M. lutulenta.* However, it is difficult to assess the affinities of *pullatella* with the males still unknown. It is similar to *lutulenta* in size and sculpturing, but is much darker in the color of the vestiture. Specifically, *pullatella* females have the scopal hairs partly or entirely brown, and most of the vestiture of the head, thorax, and abdomen dark brown.

Female. Measurements and ratios: N, 14; length, 10-11 mm.; width, 3.5-4.0; wing length, M = 2.87 ± 0.105 mm.; hooks in hamulus, M = 11.14 ± 0.177; flagellar segment 1/segment 2, M = 1.85 ± 0.019.

Structure and color: Integumental color as in *subagilis* except wing membranes slightly infumate, especially apically. Structure and sculpture as in *subagilis* except as follows: clypeal surface shiny, unshagreened or extremely slightly so; galeae tessellate; max-

illary palpal ratio about 3.0:3.0:2.6:1.0, minute fifth segment may be present (present in holotype); metasomal tergum 1 punctate in basal three-fifths, punctures shallow, surface dulled by reticular shagreening, apical area impunctate, with small, relatively impunctate, anterolateral lobes; tergum 2 with basal area punctures separated mostly by half to one puncture width, surface shiny, interband zone punctures sparse, with scattered large punctures and more abundant minute punctures, separated mostly by more than three puncture widths, but irregular, apical area impunctate or with several widely separated punctures near distal pubescent band, surfaces apical and interband areas moderately dulled by fine reticulotransverse shagreening; tergum 3 similar to 2 but interband zone punctures more abundant; pygidial plate with rounded apex.

Hair: Head dark brown. Thorax usually entirely dark brown (holotype) occasionally ochraceous on metanotum, dorsal and posterior surfaces propodeum, and just behind tegulae. Metasomal vestiture usually entirely dark brown to black (holotype), rarely with tergum 1 with long basal hairs partly ochraceous, tergum 2 with basal tomentum partly pale ochraceous, and tergum 2 with distal pubescent band interrupted medially, not reaching apical margin laterally; tergum 3 with distal band not interrupted medially, not reaching apex; tergum 4 with distal band apical. Legs dark brown except as follows: scopal hairs pale brown to brown, usually paler medially on tibiae (holotype), occasionally pale ochraceous medially on tibiae and medioproximally on basitarsi.

Type Material. The holotype female and eight female paratypes were collected August 12, 1937, on *Grindelia* sp., at five miles east of Tangent, Oregon, by H. A. Scullen. An additional five female paratypes from Oregon are as follows: Corvallis: 1 female, September 15, 1909, J. C. Bridwell; 1 female, August 29, 1924, H. A. Scullen; 1 female, July 22, 1925, D. A. Wilbur. Shedd: 2 females, August 5, 1924, H. A. Scullen (Fig. 33). The holotype is in the collection of the Oregon State College at Corvallis. Paratypes are in the collections of Oregon State College, the U. S. National Museum, Washington, D. C., the Snow Entomological Museum of the University of Kansas at Lawrence, and in the author's collection.

Melissodes (Eumelissodes) pexa, n. sp.

This small species is closely related to *M. limbus* and to *M. brevipyga.* The female resembles that of *limbus* in the dark hairs of the apical areas of terga 2 and 3, but differs from the *limbus* female in having distinct round punctures in the interband zone of tergum

2 and minute but distinct punctures in the apical areas of terga 2 and 3. This female also resembles that of *humilior* from which it differs by the shiny galeae. The male resembles that of *verbesinarum* and *humilior* in having yellow maculae on the mandibular bases, a pale labrum, and shiny galeae, and is like the male of *verbesinarum* (but unlike *humilior*) in having a thick band of appressed hairs across the apex of the first tergum. The male of *pexa* differs from that of *verbesinarum* in the mesoscutum being more densely punctate and in having a broad, short pygidial plate much as in *brevipyga*.

Female. Measurements and ratios: N, 3; length, 10-11 mm.; width, 3-4 mm.; wing length, M = 2.87 ± 0.252 mm.; hooks in hamulus, M = 12.67 ± 0.333; flagellar segment 1/segment 2, M = 2.23 ± 0.029.

Structure and color: Integumental color as in *limbus* except eyes gray. Structure and sculpture as in *limbus* except as follows: clypeus with apicomedian carina absent (allotype) or weak; mesoscutum with posteromedian area punctate, punctures separated by half to one or slightly more puncture widths; metasomal tergum 1 basally with large shallow punctures separated mostly by half to one puncture width, apical area impunctate, with anterolateral lobes sparsely punctate; tergum 2 with interband zone punctures small, deep, separated mostly by one puncture width or less, apical area with minute but distinct punctures about twice diameter of appressed hairs arising from them; tergum 3 like 2 but apical area punctures more abundant.

Hair: Vestiture as in *limbus* except as follows: vertex of head with dark brown hairs abundant; mesoscutal hairs closely decumbent; tergum 1 with anterolateral lobes of apical area with abundant, short, closely appressed, simple, dark brown hairs.

Male. Measurements and ratios: N, 4; length, 9-10 mm.; width, 2.5-3.0 mm.; wing length, M = 2.79 ± 0.219 mm.; hooks in hamulus, M = 11.50 ± 0.289; flagellar segment 2/segment 1, M = 6.29 ± 0.189.

Structure and color: Integumental color as in *verbesinarum* except as follows: labrum brown with white basomedial spot one-third to one-half area of labrum in size; mandibular base yellow (holotype) or with triangular yellow spot. Structure as in *subagilis* (and *verbesinarum*) except as follows: minimum length first flagellar segment about one-seventh or one-eighth maximum

length second segment; maxillary palpal ratio about 1.7:1.0:1.2:1.2; pygidial plate as broad near base as long or slightly broader. Sculpture as in female except as follows: tergum 1 with minute punctures almost to apical margin; terga 2-4 with apical areas impunctate. Terminalia as in *agilis*, but gonostylus not capitate, short; sternum 8 with apex entire, not emarginate or only slightly so, ventral tubercle not reaching apex, slightly bidentate.

Hair: Vestiture as in *verbesinarum* except as follows: mesoscutal hairs decumbent; terga 2, 3 and 4 often with pale brown, suberect hairs in apical areas, in holotype white.

Type Material. The holotype male from Villa Ahumada, Chihuahua, México, was collected June 28, 1947, on *Lepidium alyssoides* by C. D. Michener. The allotype female from Paila, Coahuila, México, was collected August 21, 1947, by C. D. Michener. Three male and two female paratypes are as follows: Mexico: 3 males from Villa Ahumada, Chihuahua, August 14, 1951, H. E. Evans. Arizona: 1 female from Winslow, Navajo Co., August 6, 1950, and 1 female from Joseph City, Navajo Co., August 6, 1950, J. W. MacSwain (Fig. 32). The holotype and allotype are in the collection of the American Museum of Natural History, New York City. Paratypes are in the collections of the University of California at Berkeley, the Snow Entomological Museum of the University of Kansas at Lawrence, and in the author's collection.

Melissodes (Eumelissodes) monoensis, n. sp.

This small species is closely related to *M. appressa*. The female of *monoensis* is scarcely distinguishable from that of *appressa*. However, the *monoensis* females have shorter flagellar segments 3 to 9 and have longer mesoscutal hairs which are more or less acute and not short and blunt-tipped as in females of *appressa*. The male of *monoensis* is distinctive in its short antennae which resemble the antennae of the subgenus *Tachymelissodes*. In *monoensis* males the minimum length of the first flagellar segment is one-fifth to one-half the maximum length of the second segment and the flagellum barely reaches the first metasomal tergum in repose.

Female. Measurements and ratios: N, 2; length, about 11 mm.; width, about 3.5 mm.; wing length, 2.78-3.11 mm.; hooks in hamulus, 12; flagellar segment 1/segment 2, 2.13-2.19.

Structure and color: Integumental color as in *appressa* except as follows: eyes dark gray; apex of second flagellar segment and segments 3-10 yellow to red below.

Structure and sculpture as in *appressa* except as follows: clypeal punctures smaller but crowded, apicomedial carina distinct, surface slightly dulled by fine irregular shagreening; supraclypeal area shiny, with fine irregular shagreening; galeae above shiny but with fine reticular shagreening; maxillary palpal ratio about 2.8:2.0: 1.6:1.0; third flagellar segment with length equal to about four-fifths maximum width, segments 4 to 9 all distinctly shorter than broad; mesoscutum without impunctate posteromedian area (or this area very small); metasomal tergum 2 with basal area punctures separated by half to one puncture width, interband zone moderately dulled by reticular shagreening.

Hair: Head white with abundant brown on vertex. Thorax white laterally; scutellum brown fringed with white; mesoscutum with posteromedian dark brown patch somewhat less than twice size of scutellar dark area, hairs suberect, long, not blunt-tipped; tegulae without brown. Metasomal vestiture as in *appressa* except as follows: tergum 1 with small anterolateral lobes of apical area with short, closely appressed, dark brown, simple hairs; tergum 2 with apical area half as long as distal pale band medially, with one or two rows of subappressed, brown, simple hairs just distad of distal pale band, distal band touching apical margin only at extreme sides; tergum 3 like 2 but apical area not so broad.

Male. Measurements and ratios: N, 19; length, 8.5-11 mm.; width, 2.5-3.5 mm.; wing length, $M = 2.98 \pm 0.179$ mm.; hooks in hamulus, $M = 11.10 \pm 0.194$; flagellar segment 2/segment 1, $M = 2.21 \pm 0.046$.

Structure and color: Integument black except as follows: clypeus yellow except black spots at tentorial pits and reddish-brown apical margin; flagella yellow beneath, reddish brown above; mandible with apical half red; eyes gray; tarsi dark red to brown; tegulae piceous to reddish brown; wing membranes colorless or slightly yellowed, veins red to brown; marginal areas of terga 1-6 hyaline, colorless.

Antennae barely reaching first metasomal tergum in repose; minimum length first flagellar segment equals two-fifths to one-half maximum length second segment, penultimate flagellar segment about half as broad as long or shorter; maxillary palpal ratio about 2.5:2.5:2.0:0.75. Sculpture as in female except as follows: clypeal punctures indistinct; metasomal tergum 1 with basal four-fifths with deep round punctures separated mostly by one puncture width or less, somewhat sparser medially; terga 2-4 with interband zones

similarly punctate, surfaces moderately shiny, with exceedingly fine, sparse shagreening.

Gonostylus not capitate, broader in basal two-thirds than at apex, with minute hairs; gonocoxite with blunt hairs admixed with acute on inner surface near apex. Sternum 7 with median plate large, with abundant short hairs ventrally, with an inner, posterior angle, with neck short and broad. Sternum 8 as in *opuntiella* (*Tachymelissodes*) but with more abundant, shorter hairs at apex and a more prominent ventral carina which is not bilobed but bluntly rounded.

Hair: Grayish white except as follows: yellow to orange on inner surfaces tarsi and hind tibiae and ochraceous on last two mestasomal terga. Apical pale pubescent bands on terga 2-5 consist of short, highly plumose hairs, bands on terga 2 and 3 often not reaching apices of terga medially, especially on tegum 2 and especially in worn specimens, otherwise metasomal vestiture as in *appressa*.

Type Material. The holotype male, allotype female and one female paratype from Bentons Crossing, Mono County, California, were collected July 7, 1935, by F. R. Platt (Fig. 33). Thirty-two paratype males from Bentons Crossing, California, are as follows: 9 males, September 9, 1935; 23 males, September 9, 1935, M. A. Cazier and F. R. Platt. One male paratype from Hot Creek, Mono Co., was collected August 21, 1954, on *Chrysothamnus* sp. by J. Lattin. The holotype and allotype are in the collection of Prof. P. H. Timberlake of the Citrus Experiment Station, Riverside, California. Paratypes are in the collections of P. H. Timberlake, the American Museum of Natural History, New York City, the Snow Entomological Museum of the University of Kansas, Lawrence, the U. S. National Museum, Washington, D. C., the University of California at Berkeley, and in the author's collection.

Melissodes (*Eumelissodes*) *microsticta* Cockerell

Melissodes microsticta Cockerell, 1905, *in* Viereck, *et al.* Canadian Ent., vol. 37, pp. 319-321; 1906, Trans. Amer. Ent. Soc., vol. 32, pp. 76, 113; Criddle, Curran, Viereck and Bucknell, 1924, Rept. Ent. Soc. Ontario, vol. 33, p. 99.

This is a small distinctive species related to the *menuachus* group, but not closely related to any single species. The males are distinctive in having the flagella dark brown below except for a small pale spot on each segment after the second and in having the clypeus infumate posteriorly. The females are small dark bees

with shagreened galeae, dark flagella, dark inner surfaces hind basitarsi, and a narrowly interrupted distal pale band on tergum 2. The females have the dorsal thoracic hairs blunt-tipped and erect, giving them a clipped appearance.

Female. Measurements and ratios: N, 20; length, 9-11 mm.; width, 3-4 mm.; wing length, M = 3.04 ± 0.135 mm.; hooks in hamulus, M = 12.80 ± 0.268; flagellar segment 1/segment 2, M = 1.86 ± 0.019.

Structure and color: Integument black except as follows: apical half of mandible and distitarsi rufescent; eyes bluish to greenish gray; flagellar segments 3-10 dark reddish brown to black below; wing membranes slightly infumate, brownish, veins black; tergum 1 narrowly hyaline apically; tegulae piceous; tibial spurs yellow to ochraceous.

Clypeus shaped as in *coreopsis,* with large, shallow, irregular punctures separated mostly by half a puncture width, surface dulled by reticular shagreening, apicomedian carina distinct, usually half as long as clypeus or longer; supraclypeal area shiny, shagreening, if present, delicate; lateral areas vertex with small punctures separated by half to three puncture widths, surface shiny; galeae dulled above by reticular shagreening at least in apical halves, occasionally unshagreened except near tips; maxillary palpal ratio about 2.5:2.5:2.5:1.0; second flagellar segment slightly shorter than broad above. Mesoscutum with posteromedian area punctures separated by one-half to four puncture widths, peripherally punctures separated mostly by one-half to one puncture width, surface shiny, unshagreened; scutellum similar but punctures more crowded; mesepisterna with punctures separated mostly by half a puncture width or slightly more, surface shiny; propodeal surfaces dulled by dense tessellation, dorsal surface irregularly reticulorugose. Metasomal tergum 1 with basal three-fifths medially with round punctures separated mostly by one-half to one puncture width, apical area impunctate, surface shiny, extremely finely reticulotransversely shagreened; tergum 2 with basal area with small round punctures separated mostly by one puncture width, surface unshagreened, interband zone with small punctures separated mostly by one to three puncture widths, surface slightly dulled by reticulotransverse shagreening, apical area with small punctures in basal half equal to twice diameter of hairs arising from them, surface as in tergum 1; tergum 3 like 2 but interband zone punctures more abundant and apical area shorter; tergum 4 like 3 but apical area absent;

pygidial plate V-shaped, pointed apically, sides straight, slightly longer than broad at base.

Hair: Head pale ochraceous to yellow with abundant brown on vertex. Thorax white to pale ochraceous laterally; mesoscutum ochraceous to yellow with large posteromedian dark brown area extending forwards to a transverse line at anterior margins of tegulae; scutellum dark brown fringed with ochraceous; tegulae dark brown. Metasomal tergum 1 ochraceous basally, anterolateral lobes of apical area with short, subappressed, simple dark brown hairs; tergum 2 pale ochraceous basally, distal pubescent band ochraceous, narrowly interrupted medially by brown hairs, connected to basal pale band at extreme sides, interband zone with erect to suberect, dark brown, bristlelike hairs, apical area with subappressed to suberect, long, simple, dark brown hairs except in narrow glabrous apicomedian area; tergum 3 similar to 2 but basal tomentum dark brown, distal pale band uninterrupted medially and reaching apex of tergum at least in lateral fourths, and apical area shorter and reduced to almost absent; tergum 4 like 3 but apical area absent, occasionally with dark brown apical fringe in median fourth or less; terga 5 and 6 dark brown, tergum 5 occasionally with small ochraceous lateral tufts; sterna brown to ochraceous laterally. Legs ochraceous except as follows: fore and middle tarsi, outer-apical surfaces fore and middle tibiae, and basitibial plates brown; inner surfaces hind basitarsi dark brown to black; inner surfaces hind tibiae yellow.

Male. Measurements and ratios: N, 20; length, 8-12 mm.; width, 2.3-3.5 mm.; wing length, M = 2.91 ± 0.180 mm.; hooks in hamulus, M = 11.30 ± 0.242; flagellar segment 2/segment 1, M = 5.71 ± 0.143.

Structure and color: Integument black except as follows: apical half of mandible and distitarsi rufescent; flagellar segments 3-11 reddish brown to black below with small round ventrolateral rufescent spot on each; clypeus yellow with brown apical margin and black posterior third to two-thirds; eyes dark gray to bluish or greenish gray; wing membranes slightly infumate to colorless or slightly milky, veins dark reddish brown to black; tegulae often rufescent; metasomal terga with apical areas hyaline, colorless to yellowish brown.

Clypeus as in *corcopsis;* minimum length first flagellar segment equals about one-fifth to one-seventh maximum length second segment, penultimate segment less than three times as long as

minimum width, flagellum reaching pterostigma in repose; maxillary palpal ratio about 7:6:6:1; sternum 6 with subapical oblique carinae indistinct or absent. Sculpture as in female except as follows: galeae often unshagreened except near tips; tergum 1 with basal five-sixths or more punctate; terga 3-5 similar to 2 but apical areas progressively shorter; terga 2-5 with interband zones with slightly larger punctures and apical areas virtually impunctate. Terminalia as in *agilis;* spatha short, less than 3 times as long as broad (Figs. 115-117).

Hair: Head white to pale ochraceous with abundant brown on vertex. Thorax as in female but pale hairs usually white and mesoscutal dark patch smaller, usually no more than twice size of scutellar dark area. Metasomal tergum 1 white basally and to apex at sides, apicomedially with short, simple, dark brown hairs to apex; tergum 2 white basally, distal pale band white, reaching apex and connected to basal pale band at extreme sides, medially subequal in length to apical area, interband zone with suberect to erect, white to brown, bristlelike hairs, apical area with long, subappressed to suberect, dark brown hairs; terga 3-5 similar to 2 but basal tomentum brown, interband zones often with some diffuse white pubescence, apical areas shorter or absent; terga 6 and 7 yellow to pale brown; sterna yellow to white. Legs white except inner surfaces tarsi yellow.

Bionomics. M. microsticta is an oligolege of the Compositae. Out of a total of 60 collections (65 females and 39 males) bearing floral data, 55 collections (61 females and 28 males) were from some species of composite. However, no single genus seems to be preferred. In the Pacific Coast parts of the range, the genera *Aster, Solidago, Erigeron, Gutierrezia,* and *Chrysothamnus* were most often visited by these bees, whereas in the Utah-Wyoming area *Grindelia, Helianthus* and *Solidago* were the most frequently visited genera.

Type Material. The holotype male of *microsticta* from Vancouver Island, British Columbia, Canada, is in the collection of the Philadelphia Academy of Sciences, Philadelphia, Pennsylvania (Type No. 10407).

Distribution. M. microsticta ranges from British Columbia east to Saskatchewan and south to California, Utah and Texas (Fig. 36). It has been collected from June 1 to October 11, but mainly in July and August. In addition to the holotype 332 females and

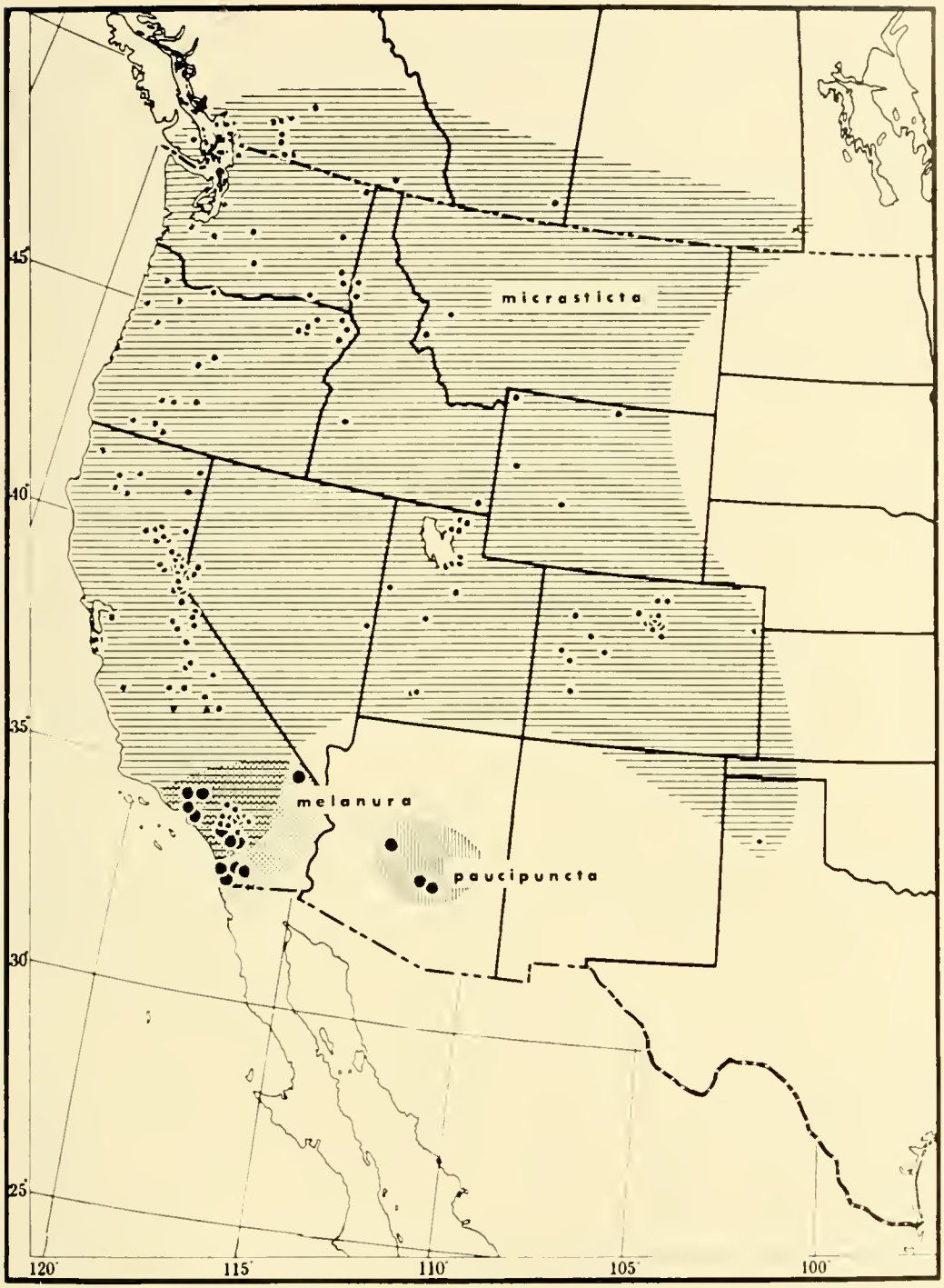


FIG. 36. Map showing the known distributions of *M. (Eumelissodes) microsticta* Cockerell, *M. (E.) melanura* (Cockerell), and *M. (E.) paucipuncta* LaBerge.

319 males have been examined from the localities listed below (including the type locality).

CALIFORNIA: Alta Mesa; Antioch; Bardon Flats; Big Bear Valley; Big Pine Camp, Inyo Co.; Blairsden, Plumas Co.; Bluff Lake, San Bernardino Mts.; Boca, Nevada Co.; Bridge Creek Camp, Lassen

Co.; Buck Creek, Modoc Co.; Butte Meadows, Butte Co.; Butterfly Valley, Plumas Co.; Calpine, Sierra Co.; Camp Lake, Tuolumne Co.; Carson Pass; Cisco; Cuyanoca (3.3 miles S.); Dodge Ridge, Tuolumne Co.; Donner Lake, Placer Co.; Dunsmuir; Echo Lake, Eldorado Co.; Eleanor Lake, Tuolumne Co.; Fallen Leaf Lake, Eldorado Co.; Felton Station, Santa Cruz Co.; Florence Lake, Fresno Co.; Giant Forest, Tulare Co.; Glacier Lodge (Big Pine), Inyo Co.; Gold Lake, Sierra Co.; Grout Creek, San Bernardino Mts.; Hobart Mills (and 7 miles N.), Nevada Co.; Hope Valley, Alpine Co.; Huntington Lake, Fresno Co.; Idyllwild; Independence Lake, Sierra Co.; Inyo Mts.; Kings River Canyon, Fresno Co.; Laguna Mt.; Lake Almanor, Plumas Co.; Lake Forest (Lake Tahoe); Lake Tahoe; Leevining; Lloyds, Tulare Co.; Meadow Valley, Plumas Co.; Mill Creek, San Bernardino Mts.; Mineralking; Mono Hot Springs, Fresno Co.; Old Station, Shasta Co.; Onion Valley, Plumas Co.; Pinecrest, Tuolumne Co.; Pine Knot, Bear Lake, San Bernardino Co.; Quincy (4 miles W.); Rathbon Creek, San Bernardino Co.; Riverside; Robinson Creek, San Bernardino Mts.; Sagehen (near Hobart Mills); Santa Ana River, San Bernardino Co.; Sequoia National Park; Shaver Lake, Fresno Co.; Sierraville; Sky Forest, San Bernardino Mts.; South Fork Camp, San Bernardino Mts.; Summit Camp, Lassen Co.; Trinity Center; Trinity River Camp, Trinity Co.; Valley of the Falls; Webber Lake, Sierra Co.; Yallao Lake, Tahoe Co.; Yosemite National Park; Yuba Pass, Sierra Nevada. COLORADO: Aspen; Boulder; Boulder Canyon; Boulder Co.; Cederedge (5 miles N.); Fort Collins; Glenwood Springs; Granby Res., Grand Co.; Jim Creek (near Boulder); Meeker; Mesa (8 miles S.); Nederland; Peaceful Valley; Pingree Park; Poudre Canyon (W. of Fort Collins); Ridgway; Science Lodge (W. of Boulder); Tolland; Ward; Wray. IDAHO: Cub River Canyon; Franklin; Lewiston; Moscow; Paris Canyon. MONTANA: Bonner; Missoula. NEVADA: Baker; Mt. Rose, Washoe Co.; Purdy, Washoe Co.; Reno; Summit (Mt. Rose Highway); Verdi. OREGON: Anara Creek, Klamath Co.; Antelope Mt., Harney Co.; Anthony Lake, Blue Mts.; Bend; Chemult (8 miles S.); Cornucopia Creek; Crater Lake Park (near Headquarters and Ple Bridge Meadow); Elgin (3 miles S.); Ely Mt. Pass, Klamath Co.; Enterprise; Estacada (Bedford Point Lookout); Forest Grove; Grande Ronde; Hood River; Jennings Lodge; Klamath Falls; La Grande (5 miles N. and 4 miles S.); Lake of the Woods, Klamath Co.; Lick Creek Res., Wallowa National Forest; Marys Peak; Medford; Mt. Ashland; Prineville; Sheep Mt. Road,

Grant Co.; Silver Creek Park, Marion Co.; Silver Lake; Summitt Prairie; Three-sisters (Scott Lake); Wallowa Lake. Texas: Canyon. Utah: Allen Canyon; Bryce Canyon; Delta; Farmington; Lake View; Logan; Logan Canyon; Magna; Mt. Nebo; Mt. Timpanogos; Murray; Petersboro; Salt Lake City; Settlement Canyon, Tooele Co.; Soldier Swamp; Vivian Park; Wellsville; Willard. Washington: Bellingham; Buckley; Colfax; Coupeville; Liberty; Metaline Falls; Mt. Constitution; Pullman; Rochester; Seattle; Spokane; Walla Walla; Whidby Island; White Rock Spring, Cascade Mts.; Yakima. Wyoming: Bondurant; Sheridan; South Pass; Yellowstone National Park. *Canada.* Alberta: Medicine Hat. British Columbia: Agassiz; Boston Bar (5 miles S.); Comox (Pt. Holmes); Crescent; Kamloops; Kerameos; Merritt; Newgate; Nicola; Oliver; Peachland; Royal Oak; Selkirk Mts. (Beaver Mouth); Sidney; Summerland; Vancouver; Vancouver Island; Vernon; Victoria; Walhackin. Saskatchewan: Maryfield.

Flower Records. Artemesia sp., *Aster* sp., *A. adscendus, A. canescens, A. delectabilis, Calyptridium umbellatum, Carduus* sp., *Cichorium sp., C. inybus, Chrysopsis* sp., *C. villosus, Chrysothamnus* sp., *C. nauseosus, C. n. consimilis, Corethrogyne* sp., *Cryptantha intermedia, Erigeron stenophyllus, Eriogonum* sp., *Grindelia* sp., *G. squarrosa, Gutierrezia californica, G. sarothrae, Haplopappus* sp., *Helenium bigelovii, Helianthus* sp., *Hemizonia wrighti, Malvastrum paniculatum, Penstemon* sp., *Phacelia* sp., *P. humilis, Senecio ionophyllus, Solidago* sp., S. *occidentalis, Sphaeralcea fasciculata.*

Melissodes (Eumelissodes) paulula, n. sp.

This small species is related to *M. microsticta.* The male of *paulula* is distinctive in that flagellar segments 4 to 11 (and often 3) have the upper-outer surfaces longitudinally depressed or flattened and very shiny (much as in certain species of the subgenus *Callimelissodes*). The male has a partially darkened clypeus and shiny galeae. The female is less easily recognized. The female of *paulula* is small, with shiny galeae, fox-red pale mesoscutal hairs, dark brown hairs on tegulae, in apical areas of terga 2 and 3 and on inner surfaces of the hind basitarsi, and has the distal pale band of tergum 2 interrupted medially with the two resulting lateral parts forming oblique fasciae tapering medially.

Female. Measurements and ratios: N, 20; length, 8-10 mm.; width, 3-4 mm.; wing length, M = 2.75 ± 0.111 mm.; hooks in hamulus, M = 11.80 ± 0.117; flagellar segment 1/segment 2, M = 1.92 ± 0.002.

Structure and color: Integumental color as in *microsticta* but wing membranes colorless to slightly milky and tergum 1 with apical area usually rufescent.

Structure and sculpture as in *microsticta* except as follows: clypeus with apicomedian carina absent or indistinct; galeae above shiny, unshagreened except near tips, with course punctation; maxillary palpal ratio about 2.5:1.7:1.7:1.0, last segment often shorter; mesoscutum with posteromedian area punctures separated mostly by one to four puncture widths, surface often with fine reticular shagreening, but scarcely dulled; metasomal tergum 2 with basal area punctures separated by half to one puncture width, surface shiny, interband zone punctures deep, large, separated mostly by half to one puncture width (often by 2 widths medially), surface slightly dulled by reticular shagreening, apical area with small punctures in basal half scarcely more than twice diameter of hairs arising from them, surface shiny; tergum 3 similar to 2 but apical area shorter, interband zone absent or almost so; tergum 4 like 3 but apical area absent; pygidial plate V-shaped but with apex more rounded than in *microsticta*, longer than basal breadth.

Hair: Vestiture as in *microsticta* except as follows: mesoscutum with pale hairs dark ochraceous to fox-red, dark posteromedian patch not reaching a transverse line at anterior margins of tegulae, not larger than twice area of scutellar dark patch; thoracic hairs blunt-tipped giving a clipped appearance above; metasomal pubescent bands white to pale ochraceous; tergum 2 with distal pale band interrupted medially with lateral parts tapering mesad to form oblique lateral fasciae, interband zone with brown hairs appressed to suberect, apical area with dark brown hairs closely appressed; tergum 3 similar to 2 but basal tomentum dark brown, interband zone virtually lacking, distal pale band broad, uninterrupted, reaching apex laterally; tergum 4 without brown apicomedially; terga 5 and 6 with lateral white tufts; legs with inner surfaces hind basitarsi dark brownish red to black.

Male. Measurements and ratios: N, 20; length 8-10 mm.; width, 2.0-2.5 mm.; wing length, $M = 2.62 \pm 0.124$ mm.; hooks in hamulus, $M = 10.45 \pm 0.198$; flagellar segment 2/segment 1, $M = 6.25 \pm 0.089$.

Structure and color: Integumental color as in *microsticta* except as follows: flagellum yellow to red below except segment 1; wing membranes colorless to slightly milky; tegulae piceous; tergal apices piceous.

Structure as in *microsticta* except as follows: minimum length first flagellar segment equals about one-sixth (holotype) maximum length second segment, penultimate segment more than three times as long as minimum width, flagellum in repose surpassing pterostigma, segments 4 to 11 (and often 3) with upper-outer surfaces longitudinally depressed or flattened and extremely shiny (these depressions located at conjunction of yellow and dark brown areas of each segment); maxillary palpal ratio about 2.2:2.0:2.0:1.0. Sculpture as in female except as follows: clypeal punctures shallow; mesoscutum often with impunctate posteromedian area; tergum 1 punctate almost to apical margin but punctures in apical third smaller and separated mostly by two or more puncture widths; tergum 2 with basal area punctures separated by half to one or slightly more puncture widths, interband zone punctures separated mostly by one to two puncture widths, apical area usually with minute punctures almost to apical margin; terga 3-5 similar to 2 but apical areas progressively shorter to absent and interband zone punctures more abundant. Sternum 6 with subapical oblique carinae strong, converging apically but not meeting. Terminalia as in *agilis* and *microsticta*.

Hair: Vestiture as in *microsticta* except as follows: tegulae often without brown; tergum 2 with distal pale band subequal to or shorter than apical area medially, interband zone hairs suberect to erect, dark-brown; terga 6 and 7 pale to dark brown, paler laterally.

Bionomics. *M. paulula* is an oligolege of the Compositae and seems to prefer the genera *Isocoma, Gutierrezia,* and *Solidago* in that order. The floral data are summarized in Table XVIII.

Type Material. Holotype male, allotype female, and seven male and seven female paratypes from Sacramento, California, were collected by Lawrence Bruner, October 3, 1916. In addition, fourteen female and three male paratypes were collected by Bruner in 1916 in the same locality as follows: September 18, 3 females; October 1, 8 females and 1 male; October 6, 3 females and 2 males. The holotype and allotype are in the collection of the Nebraska State Museum, Entomology Division, University of Nebraska in Lincoln. Paratypes are in the collections of the Nebraska State Museum, the Snow Entomological Museum of the University of Kansas, Lawrence, the U. S. National Museum, and in the author's collection.

Distribution. *M. paulula* is known only from California except for one male from the state of Washington (Fig. 37). It has been collected from July 12 to November 9, but mainly in September and

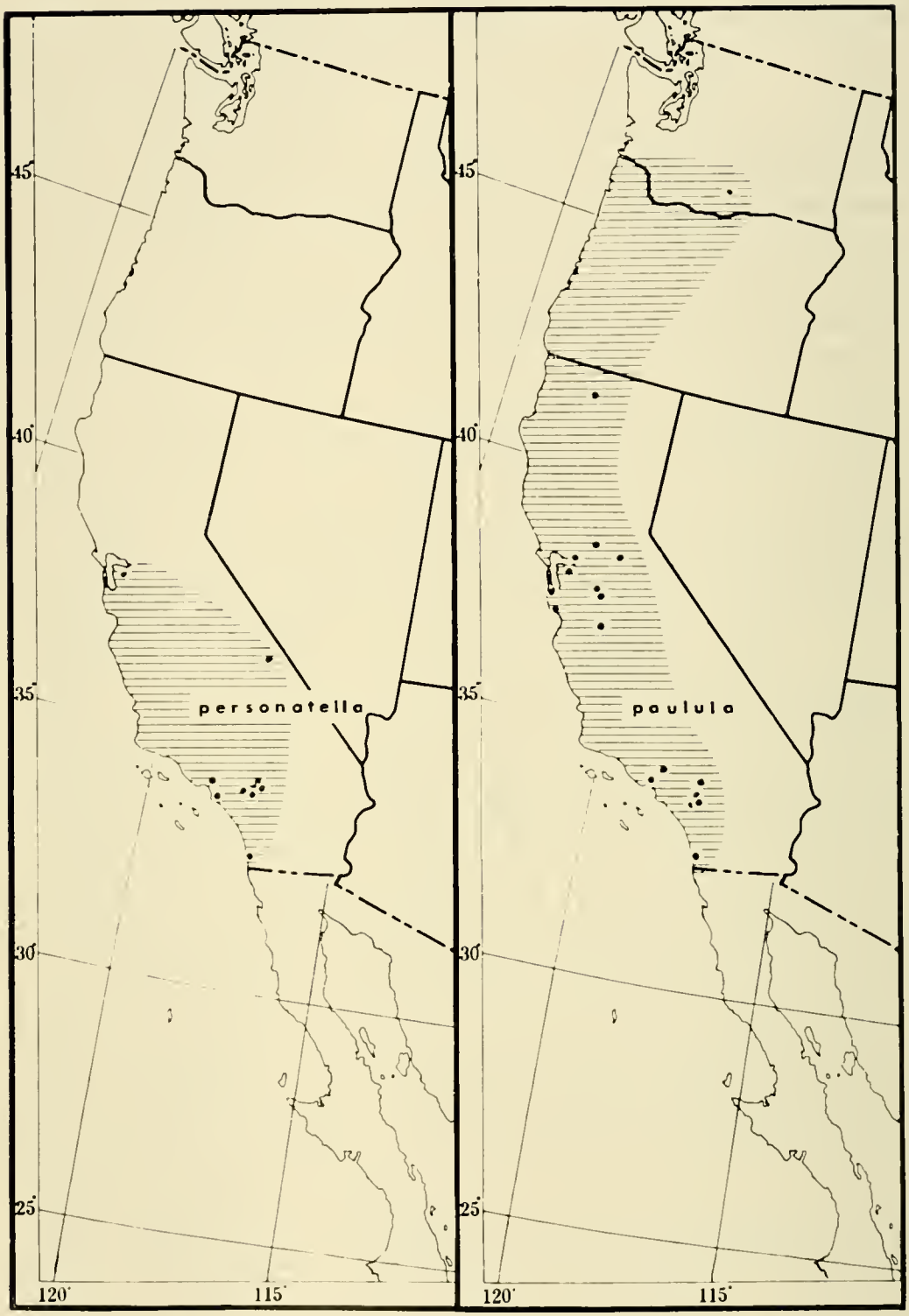


FIG. 37. Map showing the known distributions of *M. (Eumelissodes) personatella* Cockerell and *M. (E.) paulula* LaBerge.

TABLE XVIII. Summary of Floral Data for *Melissodes paulula*.

Plant Data			Records of *M. paulula*			
FAMILY	Number of genera	Number of species	Number of collections	Number of females	Number of males	Total number of bees
Compositae:						
Isocoma spp.	1	2	46	91	48	139
Gutierrezia spp.	1	2	45	47	26	73
Solidago spp.	1	2	31	39	45	84
Other genera	9	10	17	13	15	28
Other families (2)	2	2	3	0	4	4
Totals	14	18	142	190	138	328

October. In addition to the type material, 258 females and 133 males have been examined from the localities listed below (including the type locality).

CALIFORNIA: Antioch; Arcadia; Davis; Dos Palos; (6.5 miles E.); Felton Station, Santa Cruz Co.; Gazelle, Siskiyou Co.; La Sierra, Riverside Co.; Los Angeles Co.; Mission Valley; Modesto; Murphys, Calaveras Co.; Palo Alto; Redlands; Riverside; Riviera; Sacramento; San Diego; Turlock; Warm Spring (2 miles S. and 5 miles N.); Warners Ranch; Victorville. WASHINGTON: Toppenish.

Flower Records. Baccharis emoryi, Croton californicus, Ericameria palmeri, Erigeron canadense, Eriogonum fasciculatum, E. gracile, Gutierrezia sp., *G. californica, G. sarothrae, Helianthus annuus, Heliotropium oculatum, Heterotheca grandiflora, Isocoma acradenia, I. vernonioides, Pluchea camphorata, Salsola kali, Senecio* sp., *S. douglasii, Solidago sp., S. californica, S. occidentalis.*

Melissodes (*Eumelissodes*) *personatella* Cockerell

Melissodes personatella Cockerell, 1901, Canadian Ent. vol. 33, p. 297; 1902, Entomologist, vol. 32, p. 75; 1903 Psyche, vol. 10, p. 77; 1906, Trans. Amer. Ent. Soc., vol. 32, p. 75.

This small species is closely related to *M. microsticta*. The female can be distinguished from that of *microsticta* by the pale distal band of tergum 2 being uninterrupted medially, the unsha-

greened galeae, and the orange-red to red hairs of the inner surfaces of the hind basitarsi. The male of *personatella* can be distinguished from that of *microsticta* by the paler flagella without depressions as in *paulula* and with longer penultimate segments than in *microsticta*, the completely black clypeus (almost always so), and the shiny galeae.

Female. Measurements and ratios: N, 20; length, 9-11 mm.; width, 3.5-4.0 mm.; wing length, M = 2.85 ± 0.399 mm.; hooks in hamulus, M = 13.10 ± 0.176; flagellar segment 1/segment 2, M = 2.01 ± 0.003.

Structure and color: Integumental color as in *microsticta* except as follows: flagellar segments 3 to 10 red below; wing membranes colorless to slightly milky; terga 1-4 with apical areas usually slightly rufescent; tegulae often rufescent.

Structure and sculpture as in *microsticta* except as follows: clypeal punctures large posteriorly and separated by less than half a puncture width, anteriorly half the diameter, apicomedian carina weak but usually present, surface unshagreened or only delicately so; supraclypeal area shiny; lateral areas vertex with punctures minute, separated mostly by one to four puncture widths or more, surface shiny; galeae unshagreened above except near tips; maxillary palpal ratio about 3.5:3.0:2.5:1.0; mesoscutum with posteromedian impunctate area reduced to extremely small size or absent, punctures separated mostly by one to two puncture widths posteromedially except in impunctate area when present, surface slightly dulled by fine reticular shagreening; metasomal tergum 2 with basal area punctures minute, separated mostly by one puncture width, surface moderately dulled by fine reticular shagreening, interband zone punctures small, separated mostly by one to two puncture widths, surface moderately dulled by reticular shagreening, apical area impunctate or with minute sparse punctures, shiny, reticulotransversely shagreened; tergum 3 similar to 2 but apical area usually reduced to about one-third width of tergum and half length of that of tergum 2; pygidial plate V-shaped with well-rounded apex.

Hair: Vestiture as in *microsticta* except as follows: thorax with pale hairs of dorsum yellow to fox-red, mesoscutal dark patch not extending forwards to a transverse line at anterior margins of tegulae and usually no larger than twice scutellar dark area, hairs of dorsum erect and blunt-tipped giving clipped appearance; metasomal tergum 1 with apical area with abundant, short, dark brown,

closely appressed, simple hairs; tergum 2 with distal pale band pale ochraceous, uninterrupted, about twice length of apical area medially; tergum 3 similar but distal pale band reaching apical margin in lateral thirds or more, apical area shorter than in tergum 2; tergum 4 without apicomedian brown hairs; terga 5 and 6 with large pale lateral tufts; sterna yellow to yellow-brown medially and white apically and laterally; legs as in *microsticta* but inner surfaces hind basitarsi yellow-red to red.

Male. Measurements and ratios: N, 20; length, 9-11 mm.; width, 2.5-3.0 mm.; wing length, M = 2.83 ± 0.116 mm.; hooks in hamulus, M = 11.95 ± 0.158; flagellar segment 2/segment 1, M = 6.27 ± 0.093.

Structure and color: Integumental color as in *microsticta* except as follows: flagellar segments 3-11 red below; clypeus entirely black (in two specimens a small apicomedian yellow spot less than one-fourth area of clypeus present and in a third specimen clypeus mostly yellow, but blackened along posterior margin); wing membranes colorless to slightly milky; tergal apices colorless to yellowish.

Structure as in *microsticta* except as follows: minimum length first flagellar segment equals about one-sixth maximum length second segment, penultimate segment slightly more than three times as long as broad, in repose flagellum surpasses pterostigma; maxillary palpal ratio about 2.7:2.0:2.0:1.0. Sculpture as in female except as follows: clypeal punctures smaller; tergum 1 with punctures almost to apex but in apical third minute and separated mostly by two or more puncture widths; tergum 2 with basal area punctures separated mostly by half to two puncture widths, surface shiny, slightly shagreened, apical area impunctate; terga 3-5 similar to 2 but interband zone punctures more crowded and apical areas progressively shorter to absent. Terminalia as in *agilis* and *microsticta* (Figs. 120-121).

Hair: Vestiture as in *microsticta* except as follows: metasomal tergum 1 with apicomedian brown simple hairs long, subappressed to suberect; tergum 2 with distal pale band subequal to or longer than apical area medially, interband zone hairs long, suberect to erect, dark brown, bristlelike, apical area hairs long, suberect, dark brown, bristlelike; terga 3-5 similar to 2 but brown basally and apical areas shorter to absent; terga 6 and 7 yellowish to dark ochraceous.

Bionomics. M. personatella seems to be an oligolege of the composite genus *Gutierrezia.* Out of 100 available collections (106 females and 40 males) with floral data, a total of 85 collections (96 females and 35 males) were made from *Gutierrezia.* The remaining 15 collections were made from seven other composite genera and one from a plant of another family. Among these last 15 collections only *Ericameria* (Compositae) is of any importance. A single female has been seen from Guatemala. As *personatella* is otherwise known only from Californian material, it is assumed that it occurs in intervening areas as well. However, the Guatemalan record may represent a female of a new species closely related to *personatella.*

Type Material. The holotype male of *personatella* from La Jolla, California, collected in August by T. D. A. Cockerell, is in the collection of the U. S. National Museum (U. S. N. M. Type No. 13189), Washington, D. C.

Distribution. M. personatella is known from California, and by a single female from Guatemala (Fig. 37). It has been taken from May 30 to November 19, but chiefly in September and October. In addition to the holotype, 116 females and 42 males have been examined from the localities listed below.

CALIFORNIA: Altadena; Antioch; Big Bear Lake, San Bernardino Mts.; Bluff Lake, San Bernardino Mts.; La Jolla; Los Angeles Co.; Panamint Mts.; Inyo Co.; Ripley (7 miles S.); Riverside; Santa Ana Canyon, San Bernardino Co.; Santa Monica. GUATEMALA: Jicaro.

Flower Records. Ericameria palmeri, Eriogonum gracile, Gutierrezia californica, G. sarothrae, Hagardia squamosa, Helianthus sp., *Hemizonia paniculata, Heterotheca grandiflora, Isocoma vernonioides, Palofoxia linearis.*

Melissodes (*Eumelissodes*) *melanura* (Cockerell)

Exomalopsis melanurus Cockerell, 1916, Pomona Jour. Ent. Zool., vol. 8, p. 59; Bray, 1917, Pomona Jour. Ent. Zool., vol. 9, p. 95.
Melissodes melanura, Michener, 1951, *in* Museback *et al.* Hymenoptera of America north of Mexico, synoptic catalog, U. S. Dept. Agric., Agric. Monogr. No. 2, p. 1226.

This small species is related to *M. microsticta.* The female is readily identified by the long galeal hairs which are hooked near the tips, the densely tessellate galeae, the broad metasomal bands, and the small size. The male of *melanura* has a black clypeus as in *personatella,* densely tessellate galeae, metasomal bands as in the female, long flagella which are strongly crenulate especially in the

last four to six segments, and strong subapical carinae on the sixth sternum.

Female. Measurements and ratios: N, 20; length 8-10 mm.; width, 3.0-3.5 mm.; wing length, M = 2.41 ± 0.086 mm.; hooks in hamulus, M = 11.30 ± 0.128; flagellar segment 1/segment 2, M = 1.98 ± 0.017.

Structure and color: Integumental color as in *microsticta* except as follows: eyes bluish to greenish gray; flagellar segments 3-10 red below; wing membranes milky, veins dark reddish brown; tegulae and tergal apices usually rufescent.

Structure and sculpture as in *microsticta* except as follows: clypeal surface shiny, unshagreened; galeae opaque, densely tessellate, with abundant long hairs hooked near tips; mesoscutum with posteromedian area impunctate or nearly so, elsewhere punctures large, separated by one puncture width or less, surface shiny; metasomal tergum 1 with basal half or slightly more with coarse punctures separated mostly by half a puncture width or slightly more, apical area with minute wide-spread punctures except near apex; tergum 2 with basal area punctures separated by half to one puncture width, surface shiny, interband zone with small punctures regularly spaced by half to one puncture width, surface moderately dulled by fine reticular shagreening, apical area impunctate or with minute punctures; tergum 3 like 2 but apical area equals no more than one-third width of tergum and shorter than in 2; tergum 4 like 3 but lacking apical area; pygidial plate with apex rounded.

Hair: Head white on lower parts to ochraceous above with abundant brown on vertex. Thorax white laterally to ochraceous above except mesoscutum with posteromedian dark brown patch about twice size of scutellar dark patch; hairs of dorsum short, blunt-tipped, giving clipped appearance. Metasomal tergum 1 white to pale ochraceous basally, apical area, and especially anterolateral lobes of apical area, with short, closely appressed, dark brown, simple hairs; tergum 2 with basal white band connected at extreme sides to distal white band, distal band uninterrupted, subequal in length to interband zone medially (interband zone of about same length across entire tergum) and twice length of apical area, interband zone hairs abundant, appressed to subappressed, dark brown, apical area hairs sparse, appressed to subappressed, dark brown; tergum 3 similar to 2 but basal tomentum dark brown and apical area reduced to one-third width of tergum or less and shorter; tergum 4 like 3 but lacking apical area; terga 5 and 6 brown to dark

brown with pale lateral tufts; sterna yellow or white medially, white apically and laterally. Legs as in *microsticta* but inner surfaces hind basitarsi yellow to red and scopae white.

Male. Measurements and ratios: N, 20; length, 7-10 mm.; width 2-3 mm.; wing length, M = 2.32 ± 0.132 mm.; hooks in hamulus, M = 9.60 ± 0.184; flagellar segment 2/segment 1, M = 6.83 ± 0.983.

Structure and color: Integumental color as in *microsticta* except as follows: clypeus from entirely black (13 specimens) to two-thirds yellow (one specimen), usually less than half yellow, if at all; flagellar segments 2-11 yellow to red below; eyes greenish to bluish gray; wing membranes milky; tergal apices hyaline and colorless to translucent brown.

Structure as in *microsticta* except as follows: minimum length first flagellar segment equals about one-seventh maximum length second segment, penultimate segment more than three times as long as broad, flagellum in repose surpasses pterostigma, last four to six segments strongly crenulate above; maxillary palpal ratio about 6:6:4:1; sixth sternum with weak subapical oblique carinae. Sculpture as in female except as follows: tergum 1 punctate almost to apical margin but punctures become smaller and sparser in last fifth; terga 2-4 with interband zone punctures separated by one to two puncture widths or slightly more. Terminalia as in *agilis* and *microsticta* (Figs. 122-123).

Hair: Vestiture as in female except as follows: galeal hairs abundant but not hooked near tips; tergum 1 with apical third to two-fifths with abundant, long, subappressed, dark brown, simple hairs; tergum 2 with distal pale band slightly longer than apical area medially; terga 2-5 with interband zone hairs long, suberect to subappressed, bristlelike, dark brown, and apical areas progressively shorter, with suberect to subappressed, brown hairs; terga 6 and 7 brown. Legs as in *microsticta.*

Bionomics. There is not sufficient data to warrant a statement concerning oligolecty in *M. melanura.* However, the hooked galeal hairs of the female suggest that *melanura* is adapted to some particular flower or group of flowers for sources of pollen.

Type Material. The holotype female of *melanura* from Claremont, California, collected by Baker, is in the collection of the American Museum of Natural History, New York City.

Distribution. Except for one male from Nevada, all known specimens of *melanura* are from California (Fig. 36). It has been taken

from August 12 to October 10. In addition to the holotype, 54 females and 25 males have been examined from the localities listed below.

California: Altadena; Antioch; Boquet Canyon, Angeles National Forest; Dutch Flat, San Jacinto Mts.; Felton Station, Santa Cruz Co.; Green Valley, Angeles National Forest; Hemit Valley, San Jacinto Mts.; Idyllwild; Julian; Keen Camp (3 miles E.), Riverside Co.; Los Angeles Co.; Mill Creek, San Bernardino Co.; Mission Valley; Riverside; San Diego; San Diego Co.; Warner Springs (5 miles N.). Nevada: "Nev."

Flower Records. Aster sp., *Corethrogyne* sp., *C. bernardina, Erigeron* sp., *Eriogonum virgatum, Gutierrezia california, G. sarothrae, Lessingia glandulifera, Solidago* sp.

Melissodes (*Eumelissodes*) *terminata* n. sp.

Although this species is represented by a single male from Baja California, I do not hesitate to describe it, as it is very distinctive. It is related to *microsticta* and *personatella* and has the partially blackened clypeus so common in that group. It can be easily recognized by the last two flagellar segments being black and contrasting with the preceding segment which is yellow below.

Male. Measurements and ratio: N, 1; length, about 10 mm.; width, about 3 mm.; wing length, 3.27 mm.; hooks in hamulus, 12; flagellar segment 2/segment 1, 6.78.

Structure and color: Integumental color as in *microsticta* except as follows: clypeus black with subapical trilobed yellow macula covering slightly more than half of clypeus; mandibles and labrum black; flagellum yellow-orange below, dark brown above except first segment entirely brown and last two segments black; tergal apices translucent brown.

Structure as in *microsticta* except as follows: minimum length of first flagellar segment about six and two-thirds maximum length second segment, penultimate segment more than three times as long as broad, flagellum in repose surpassing pterostigma; maxillary palpal ratio about 3.5:3.0:3.0:1.0; sternum 6 with subapical oblique carinae sharp, distinct, curved, slightly less than twice as long as distance between their tips, with well-developed median sulcus, apex emarginate. Sculpture as in *microsticta* except terga 2-5 with interband zone punctures separated mostly by one to two puncture widths and surfaces dulled by reticular shagreening. Sternum 7 with median plates with a transverse ventral ridge

supporting several rows of long hairs clearly separating the apical puberulent plate from the basal, shiny, apubescent neck region. Sternum 8 with apicomedian ventral tubercle sharply pointed, apical margin strongly emarginate medially with the two lateral apical lobes with sharp apices. Genital capsule as in *agilis,* gonostyli slightly capitate, with abundant short hairs especially basally.

Hair: Head and thorax as in *microsticta* but brown hairs of vertex less abundant and tegulae without brown. Metasomal vestiture as in *microsticta* except as follows: tergum 1 with apicomedian area with few simple brown hairs; tergum 2 with interband zone hairs white, apical area hairs white and sparse; terga 6 and 7 pale ochraceous; sternal hairs yellow medially to white basally. Legs as in *microsticta.*

Type Material. The holotype male from 32 miles south of Tijuana, Baja California, Mexico, collected on July 31, 1934, by Basinger, is in the collection of Prof. P. H. Timberlake of the Citrus Experiment Station, Riverside, California.

Remarks. M. terminata was first recognized as a new species by P. H. Timberlake. The blackened apical flagellar segments, so distinctive in this specimen, may be merely a monstrosity. However, there are no other indications that this is the case on this specimen.

Melissodes (*Eumelissodes*) *micheneri,* n. sp.

This is a distinctive, medium-sized bee from California. It is not closely related to the foregoing species, but, perhaps, is most closely related to *M. melanura.* The female can be recognized by the acutely pointed pygidial plate, the dulled galeae, and the relatively long second flagellar segments. The males are readily recognized by the dark antennae (as in *microsticta*), the black clypeus, the dull galeae, and the sharp and long subapical carinae of the sixth sternum. This species is named in honor of Dr. C. D. Michener of the University of Kansas who collected the holotype and to whom the author is indebted for time and advice during the progress of this revision.

Female. Measurements and ratios: N, 20; length, 10-13 mm.; width, 3.5-4.5 mm.; wing length, M = 3.62 ± 0.123 mm.; hooks in hamulus, M = 13.90 ± 0.239; flagellar segment 1/segment 2, M = 1.60 ± 0.002.

Structure and color: Integumental color as in *microsticta* except as follows: eyes gray; wing membranes colorless, veins black.

Structure and sculpture as in *microsticta* except as follows: clypeal punctures round, separated by half a puncture width, surface and bottoms of punctures tessellate; supraclypeal area moderately dulled by irregular shagreening; galeae dulled above by fine tessellation; maxillary palpal ratio about 2.7:2.3:1.7:1.0; second flagellar segment distinctly longer than maximum width (ratio of width/length about 5/6 in allotype); mesoscutum with posteromedian area punctures separated mostly by one to two puncture widths, surface often with fine reticular shagreening but not dull; scutellum with punctures small, separated mostly by one to three puncture widths, surface as in mesoscutum; metasomal tergum 1 with basal four-fifths with small round punctures separated mostly by half to two puncture widths; tergum 2 with basal area punctures separated by one puncture width or more, surface slightly dulled by delicate shagreening, interband zone punctures minute, shallow and indistinct, separated mostly by two to four puncture widths, surface dulled by fine dense reticulotransverse shagreening, apical area impunctate; tergum 3 similar to 2 but interband zone punctures denser and more distinct; pygidial plate V-shaped with apex acutely pointed and sides usually slightly concave to straight, longer than basal breadth.

Hair: Head pale ochraceous to yellow with abundant dark brown on vertex. Thorax pale ochraceous to yellow laterally; scutellum dark brown medially, yellow peripherally; mescoscutum with dark brown posteromedial area no larger than twice scuteller dark area and usually smaller, peripherally yellowish-ochre to dull rufescent; tegulae with dark brown. Metasomal tergum 1 pale ochraceous basally, glabrous apically; tergum 2 pale ochraceous to white basally, distal pale band pale ochraceous, composed of long pubescence, not interrupted medially, almost reaching apex of tergum laterally, interband zone with long, erect, pale ochraceous hair, apical area (unless worn) with long, simple, dark brown, suberect hairs; tergum 3 similar to 2 but basal tomentum dark brown and distal pale band reaching apex in lateral thirds; tergum 4 like 3 but apical area absent; terga 5 and 6 dark brown with pale lateral tufts at least on 5; sterna dark brown, white laterally and along apical margin of penultimate sternum. Legs as in *microsticta*.

Male. Measurements and ratios: N, 20; length, 9-13 mm.; width, 2.5-3.5 mm.; wing length, $M = 3.21 \pm 0.162$ mm.; hooks in hamulus. $M = 12.35 \pm 0.131$; flagellar segment 2/segment 1, $M = 7.45 \pm 0.100$.

Structure and color: Integumental color as in *microsticta* except as follows: clypeus entirely black; wing membranes colorless, veins dark brown; tergal apices piceous.

Structure as in *microsticta* except as follows: minimum length first flagellar segment about one-ninth to one-tenth (holotype) maximum length second segment, penultimate segment slightly more than three times as long as broad, in repose surpassing pterostigma; maxillary palpal ratio about 2.7:2.3:2.0:1.0; sternum 6 with distinct, sharp, subapical carinae converging distally, each carina about twice length of distance between their tips, sternum flat between carinae, without well-marked median sulcus, but often shiny medially. Sculpture as in female except as follows: metasomal tergum 1 with punctures almost to apical margin but smaller and sparser in apical fifth; terga 3-5 similar to 2 but apical areas progressively shorter. Terminalia as in *agilis* but gonostylus extremely slender, long, more than ⅓ length of gonocoxite, hairless; sternum 7 with median plate produced apicolaterally; sternum 8 with ventral tubercle not bidentate.

Hair: Head and thorax as in female but pale hairs of thoracic dorsum usually pale ochraceous. Metasomal vestiture as in female except as follows: tergum 1 with apical area with abundant, suberect, simple, dark brown hairs; tergum 2 with distal pale band shorter and interband zone hairs dark brown; terga 3-5 similar to 2 but apical areas progressively shorter (often lacking completely on 5); terga 6 and 7 brown; sterna yellow to brown medially, pale ochraceous to white laterally. Legs pale ochraceous to white except inner surfaces tarsi yellow.

Remarks. M. micheneri is an oligolege of the Compositae and seems to prefer the genera *Chrysothamnus* and *Chrysopsis.* Out of a total of 20 collections available with floral data (100 females and 76 males), 11 were taken from *Chrysothamnus* (50 females and 11 males) and 9 from *Chrysopsis* (50 females and 65 males).

Type Material. The holotype male and allotype female from Mill Creek, San Bernardino Co., California, were collected by C. D. Michener, August 31, 1930. In addition, 44 female and 19 male paratypes from San Bernardino Co., California, are as follows: Forest Home (Mill Creek Canyon): 19 females and 3 males on *Chrysothamnus* sp., September 22, 1935, P. H. Timberlake; 3 males, August 22, 1953, J. C. Hall. Mill Creek: 1 male, September 1, 1930, C. D. Michener; 2 females, September 5, 1931, C. D. Michener. Also from Mill Creek collected by P. H. Timberlake; 7 males on *Chrysopsis*

fastigiata, August 15, 1934; 3 females and 4 males on *C. fastigiata,* August 24, 1936; 9 females and 1 male on *Chrysopsis villosa,* September 5, 1937; 2 females on *Chrysothamnus* sp., September 19, 1937; 1 female on *Chrysothamus* sp., August 21, 1942; 3 females on *C. villosa,* August 21, 1942; 2 females on *Chrysothamnus* sp., September 10, 1945; 3 females on *C. villosa,* September 1, 1947. The holotype and allotype are in the Snow Entomological Museum of the University of Kansas, Lawrence. Paratypes are in the collections of the Snow Entomological Museum, P. H. Timberlake of the Citrus Experiment Station, Riverside, California, the University of California at Davis, the California Academy of Sciences, San Francisco, the U. S. National Museum, Washington, D. C., and in the author's collection.

Distribution. M. micheneri is known only from California (Fig. 32). It has been collected only in August and September. In addition to the type material, 64 females and 65 males have been examined from the localities listed below (this list includes the type localities).

California: Big Trees, Calaveras Co.; Convict Lake, Mono Co.; Forest Home, Mill Creek Canyon; Mill Creek, San Bernardino Co.; Murphys, Calaveras Co.; Pinecrest, Tuolumne Co.; San Diego; Valley of Falls, San Bernardino Co.

Flower Records. Chrysopsis fastigiata, C. villosa, Chrysothamnus sp.

Melissodes (Eumelissodes) moorei Cockerell

Melissodes moorei Cockerell, 1926, Ann. Mag. Nat. Hist., ser. 9, vol. 18, p. 624.

M. moorei is closely related to *M. micheneri.* The female of *moorei* differs from that of *micheneri* by the pygidial plate being rounded apically, the wings somewhat infuscated, the galeae having at least a few hairs bent or hooked near the tips, and small but distinct punctures in the apical areas of terga 2 and 3. This female also resembles that of *robustior,* but can be distinguished by the hooked galeal hairs and punctate tergal apices. The male of *moorei* has a black clypeus and dark flagella as in *micheneri,* but has the subapical carinae of sternum 6 only weakly developed and occasionally a small amount of yellow on the clypeus and somewhat paler flagella.

Female. Measurements and ratios: N, 19; length, 10-13 mm.; width, 4.0-4.5 mm.; wing length, $M = 3.42 \pm 0.152$ mm.; hooks in

hamulus, M = 15.90 ± 0.369; flagellar segment 1/segment 2, M = 1.86 ± 0.020.

Structure and color: Integumental color as in *microsticta* except eyes bluish to brownish gray. Structure and sculpture as in *microsticta* except as follows: clypeus with posteromedian punctures large, separated by half a puncture width, laterally and posteriorly smaller and extremely shallow, anteriorly shallow and extremely small, surface tessellate, especially peripherally and at bottoms of large punctures, apicomedian carina weak or absent; supraclypeal area with distinct reticular shagreening; galeae tessellate above, with abundant long hairs hooked or bent near tips (at least a few hooked); maxillary palpal ratio about 4.0:3.5:3.5:1.0; second flagellar segment about as long as broad or extremely slightly longer; mesoscutum, especially peripherally, with surface often dulled by fine reticular shagreening; metasomal tergum 1 medially with basal five-sixths punctate; tergum 2 with basal area punctures separated mostly by one puncture width or slightly more, surface reticularly shagreened, apical area with punctures three to four times width of hairs arising from them or more and separated mostly by two to three puncture widths, surface finely shagreened, shiny; tergum 3 similar to 2 but interband zone punctures smaller and apical area punctures more crowded; tergum 4 like 3 but apical area lacking; pygidial plate V-shaped, apex rounded, longer than broad.

Hair: Head and thorax as in *micheneri* except as follows: labrum often with brown; vertex with more abundant brown hairs; mesoscutal dark patch often twice as large as scutellar dark area or larger. Metasomal vestiture as in *micheneri* except as follows: tergum 1 with basal pale hairs decumbent and reaching apex medially, with long, suberect to subappressed, simple, dark brown hairs mixed with the pale along apical margin of punctate area; tergum 2 with distal pale band short, often narrowly interrupted medially, if not, then shorter than apical area, interband zone hairs suberect to erect, dark brown, apical area suberect brown hairs more abundant; tergum 3 similar to 2 but apical area shorter, distal pale band broader, uninterrupted, and not reaching apical margin laterally; tergum 4 like 3 but lacking apical area.

Male. Measurements and ratios: N, 20; length, 10-13 mm.; width, 3-4 mm.; wing length, M = 3.25 ± 0.134 mm.; hooks in hamulus, M = 14.45 ± 0.411; flagellar segment 2/segment 1, M = 6.39 ± 0.113.

Structure and color: Integumental color as in *microsticta*, clypeus

usually entirely black, rarely with small yellow subapical strip less than one-tenth area of clypeus; flagella below usually somewhat reddened; eyes bluish to yellowish gray; tegulae piceous; tergal apices usually slightly translucent, yellowish brown to piceous.

Structure as in *microsticta* except as follows: minimum length first flagellar segment one-eighth to one-ninth maximum length second segment, penultimate segment slightly more than three times as long as broad, reaching pterostigma in repose, segments 3 or 4 to 10 crenulated by basal constrictions; maxillary palpal ratio about 3.6:3.2:3.2:1.0; sternum 6 with subapical carinae weakly developed, each carina blunt and much shorter than half distance between their tips, median shiny sulcus present. Sculpture as in female except as follows: tergum 1 punctate to within one-eighth of apex or less, last sixth of punctate area with punctures smaller and separated mostly by less than one puncture width; tergum 2 with interband zone punctures separated by one to three puncture widths, apical area punctures smaller and sparser; terga 3 to 5 similar to 2 but apical areas progressively shorter. Terminalia as in *micheneri* but gonostylus with minute hairs, sternum 7 with median plates as in *agilis* (not produced apicolaterally), and sternum 8 with ventral tubercle dark, sclerotized and bidentate apically (Figs. 124-125).

Hair: Vestiture as in *micheneri* except as follows: tergum 2 with distal pale band usually interrupted medially; terga 3-5 similar to 2 but apical areas progressively shorter (present on 5), basal tomentum brown and distal pale bands uninterrupted.

Remarks. Not enough data are available to make a firm statement regarding the flower preferences of *M. moorei.* However, the hooked galeal hairs of the female indicate that they are adapted to one or a few plants as sources of pollen. *M. moorei* females have been collected only on *Grindelia* and *Hemizonia* and no specimens have yet been taken on any but the Compositae.

Type Material. The holotype female of *moorei* from sand hills at Pacific Grove, California, collected by Cockerell on July 3, is in the collection of Prof. P. H. Timberlake of the Citrus Experiment Station, Riverside, California.

Distribution. M. moorei is known chiefly from the coastal area of California (Fig. 31). It has been collected from June 6 to September 24, chiefly in August and September. In addition to the holotype, 21 females and 40 males were examined from the localities listed below.

California: Alpine Lake, Marin Co.; Bird Rock (near), Mon-

terey Coast; Dunsmuir; Encinitas; Grover City, San Luis Obispo Co.; Ingleside (Ocean Beach), San Francisco Co.; Los Angeles Co.; Mokelumne Hill; Mono Bay; Monterey; Naples; Pacific Grove, Monterey Co.; Palm City; Pinecrest; Pt. Pinos; Redondo Beach, Los Angeles Co.; San Francisco Co.; Santa Monica.

Flower Records. Corethrogyne sp., *Grindelia* sp., *G. platyphylla, Hemizonia peniculata, Heterotheca grandiflora, Solidago* sp.

Melissodes (Eumelissodes) exilis, n. sp.

This small species is closely related to *M. microsticta.* The female of *exilis* differs from that of *microsticta* in having the distal pale band of tergum 2 uninterrupted, the interband zone of tergum 2 with the surface dulled by dense shagreening, unshagreened galeae, and less brown hair on the mesoscutum. The male of *exilis* is like that of *microsticta* but has piceous tergal apices, longer penultimate flagellar segments and flagellum, and tergum 2 sculptured as in the female.

Female. Measurements and ratios: N, 3; length, about 11 mm.; width, about 4 mm.; wing length, $M = 3.45 \pm 0.029$ mm.; hooks in hamulus, $M = 13.00 \pm 0.577$; flagellar segment 1/segment 2, $M = 4.86 \pm 0.105$.

Structure and color: Integumental color as in *microsticta* except as follows: eyes dark bluish gray; tibial spurs ochraceous; tergum 1 piceous apically.

Structure and sculpture as in *microsticta* except as follows: clypeal punctures slightly smaller, crowded, apicomedian carina weak or absent; supraclypeal area slightly shagreened; galeae above unshagreened except near tips; tergum 1 with basal area punctures separated mostly by half to two puncture widths, surface dulled by dense reticulotransverse shagreening; tergum 2 with interband zone punctures no larger than those of basal area and separated by one to three puncture widths, surface opaque, dulled by dense reticulotransverse shagreening, apical area impunctate or with minute punctures basally, surface somewhat dulled by fine dense reticulotransverse shagreening; terga 3 and 4 similar to 2 but apical areas shorter or absent; pygidial plate as in *microsticta.*

Hair: Head pale ochraceous to yellow except as follows: labrum brown; vertex with abundant dark brown; pale hairs on or near vertex fox-red. Thorax ochraceous laterally to fox-red above except as follows: scutellum dark brown fringed with yellow; mesoscutum with dark brown posteromedian patch no more than twice area of

scutellar dark patch (less in allotype); tegulae with dark brown. Metasomal tergum 1 dark ochraceous basally, glabrous apically; tergum 2 pale ochraceous basally, distal pale band ochraceous, uninterrupted medially, as long as apical area medially, interband zone with long, relatively simple, suberect, pale ochraceous, bristle-like hairs, apical area with long, subappressed to suberect, dark brown hairs at least basally; tergum 3 similar to 2 but basal tomentum dark brown, apical area shorter and often distal pale band reaching apex at extreme sides; tergum 4 like 3 but apical area reduced to small apical triangular area one-fourth width of tergum (allotype) or absent; terga 5 and 6 dark brown; sterna dark brown with ochraceous laterally. Legs as in *microsticta*.

Male. Measurements and ratios: N, 2; length, about 10 mm.; width, about 3 mm.; wing length, 2.74-3.07 mm.; hooks in hamulus, 10-11; flagellar segment 2/segment 1, 8.05-8.68.

Structure and color: Integumental color as in *microsticta* except as follows: flagellar segments 2-11 dark reddish brown below with small ventrolateral paler spots on each; eyes dark gray; tegulae piceous; tergal apices piceous except first extremely narrowly hyaline.

Structure as in *microsticta* except as follows: minimum length first flagellar segment equals about one-eighth maximum length second penultimate segment and more than three times as long as minimum width, flagellum in repose surpassing pterostigma; maxillary palpal ratio about 3.5:3.0:2.8:1.0. Sculpture as in female except as follows: basal four-fifths of tergum 1 punctate; terga 3-5 similar to 2 but with shorter apical areas. Terminalia as in *agilis* but gonostylus slender, short (about ⅓ length of gonocoxite or less), scarcely capitate and almost hairless, and sternum 8 with ventral tubercle not bidentate; spatha almost half as long as broad.

Hair: Vestiture as in *microsticta* except as follows: vertex of head with dark brown hairs more abundant; mesoscutal dark patch twice size of scutellar dark area, broader anteriorly than posteriorly; pale hairs of mesoscutum and upper mesepisterna yellow; terga 2 and 3 with distal pale bands shorter than apical areas; terga 4 and 5 with distal pale bands broader than apical areas; terga 6 and 7 dark brown; sterna yellow to white laterally.

Type Material. The holotype male and allotype female from 15 miles north of Tucson, Arizona, were collected by G. D. Butler on *Viguiera* sp., September 14-16, 1955. In addition, two females and one male paratype from Arizona are as follows: 2 females

from 15 miles north of Tucson, on *Aster* sp., September 14-16, 1955, G. D. Butler; 1 male from Tucson, on a yellow composite, September 14, 1955, G. D. Butler (Fig. 32). The holotype and allotype are the property of the University of Arizona but are deposited on indefinite loan in the Snow Entomological Museum of the University of Kansas, Lawrence. Paratypes are in the collection of the University of Arizona, Tucson, and in the author's collection.

Melissodes (Eumelissodes) paucipuncta, n. sp.

This small species is not closely related to any of the foregoing species. It has certain resemblances to members of the *microsticta* group, however, and so is treated here. The female is distinctive in the sparseness of the metasomal punctation: the first metasomal tergum has only sparse punctures separated by about three puncture widths in the basal third or less and very few elsewhere; the interband zones and apical areas of terga 2 and 3 are virtually impunctate. Furthermore, the scopal hairs of the female are only weakly branched and some sternal hairs seem to form an accessory scopa as described below. The male is distinctive in having sparsely punctate terga as in the female (but less so), short antennae not reaching the pterostigma in repose and with the penultimate segment less than three times as long as broad, and piceous tergal apices.

Female. Measurements and ratios: N, 2; length about 10 mm.; width about 3.5 mm.; wing length, 2.97-3.11 mm.; hooks in hamulus, 12; flagellar segment 1/segment 2, 1.80-1.85.

Structure and color: Integumental color as in *microsticta* except as follows: eyes greenish gray; flagellar segments 3-10 red below; wing membranes colorless.

Structure and sculpture as in *microsticta* except as follows: clypeus more protuberant, punctures well-spaced, separated by more than half a puncture width, posteromedially by as much as one or slightly more puncture width, surface unshagreened, apicomedian carina weak; supraclypeal area punctate, shiny, irregularly shagreened; maxillary palpal ratio about 5.3:4.7:2.7:1.0; mesoscutum impunctate posteromedially, punctures surrounding impunctate area anteriorly to anterior ends of and within parapsidal lines (and slightly anterior to this medially) separated mostly by two or three puncture widths, peripherally punctures separated by one to two puncture widths, surface shiny; scutellum with small punctures separated by one to two puncture widths, surface shiny; propodeum

with dorsal surface impunctate medially, scattered small round punctures in lateral thirds, surface tessellate; metasomal tergum 1 with small punctures in basal third or less separated by two to five puncture widths, apical area impunctate; tergum 2 with basal area punctures minute, separated by one to two puncture widths, interband zone and apical areas impunctate; terga 3 and 4 similar to 2 but interband zone with several scattered punctures especially laterally near distal pale bands; pygidial plate apex rounded.

Hair: Vestiture as in *microsticta* except as follows: pale hair and pubescence white; tegulae without or with little brown; tergum 1 glabrous apically; tergum 2 with distal white band markedly interrupted medially, subequal in length (at ends of fasciae) to apical area, interband zone virtually bare, apical area and between fasciae of distal pale band with closely appressed, simple, brown hairs; tergum 3 like 2 but basal tomentum brown, distal white band only narrowly interrupted and longer than apical area, and interband zone with hair similar to apical area; tergum 4 like 3 but apical area reduced to small apicomedian triangle less than one-third width of tergum and almost glabrous; terga 5 and 6 with conspicuous white lateral tufts; sterna yellow to brown medially, white laterally, many long apicomedian hairs of first three sterna with tips curled (probably accessory scopal hairs). Legs as in *microsticta* except inner surfaces hind basitarsi yellow to red and scopal hairs with branches sparse (usually 2 or 3 on each side of rachis), long, curled near tips.

Male. Measurements and ratios: N, 2; length, about 11 mm.; width, about 3 mm.; wing length, 2.86-2.99 mm.; hooks in hamulus, 10; flagellar segment 2/segment 1, 4.52-4.92.

Structure and color: Integumental color as in *microsticta* except as follows: flagellar yellow beneath except first segment brown; eyes greenish gray; clypeus yellow except apical margin testaceous and dark maculae at tentorial pits; wing membranes clear, veins dark brown; tergal apices piceous or hyaline but smoky brown (as in allotype).

Structure as in *microsticta* except as follows: minimum length first flagellar segment equals one-sixth to one-seventh maximum length second segment, penultimate segment distinctly less than three times as long as minimum width, flagellum not reaching prestigma in repose; maxillary palpal ratio about 6.5:6.0:2.5:1.0. Sculpture as in female except as follows: tergum 1 with basal four-fifths with large shallow punctures separated by one to three puncture widths; terga 2-4 with interband zones with sparse, irregular-sized

punctures separated mostly by three or four puncture widths; tergum 5 similar but more punctate and apical area shorter. Sternum 6 with subapical oblique carinae very strong and sharp, each almost twice as long as distance between their apices. Terminalia as in *agilis* except as follows: gonostylus short (about ⅓ as long as gonocoxite), broad (almost half as broad as long), with minute hairs; sternum 7 with median plate with long neck and small, transverse apical plate which is glabrous ventrally, lateral plates small and weakly sclerotized; sternum 8 only slightly emarginate apically and with ventral tubercle acute, not bidentate.

Hair: Vestiture as in female except as follows: tergum 1 with basal four-fifths with sparse white hair; terga 2-5 with interband zones with sparse brown hairs (often ochraceous or white on tergum 2) suberect to erect, apical areas glabrous and progressively shorter; terga 3-5 with distal white band not interrupted medially; terga 6 and 7 dark brown; sterna yellow medially, white laterally; legs white with inner surfaces tarsi yellow.

Bionomics. The peculiar scopal hairs plus the probably accessory scopal hairs of the sterna of the female of *paucipuncta* suggest the adaptation to and oligolecty on flowers of *Opuntia* (Cactaceae). This is the only species of *Melissodes* in which the sternal hairs seem to be modified to aid in collecting of pollen, although these hairs must be of some service in this respect in other species.

Type Material. The holotype female from east of Thompson Arbor, Superior, Arizona, was collected May 15, 1954, on *Opuntia* sp., by G. D. Butler. The allotype male from four miles east of Apache Junction, Arizona, was collected May 15, 1954, by G. D. Butler. One paratype male was collected on *Bebbia* sp. by Butler at the same time and place as the allotype. One paratype female from ten miles northwest of Wickenburg, Arizona, was collected May 21, 1945, on *Opuntia* sp., by W. P. Cockerell. The holotype and allotype are the property of the University of Arizona but are on indefinite loan to the Snow Entomological Museum of the University of Kansas at Lawrence. One paratype (male) is in the collection of R. R. Snelling of Turlock, California and the other (female) is in the collection of P. H. Timberlake of the Citrus Experiment Station, Riverside, California.

Melissodes (Eumelissodes) crocina, n. sp.

This small brightly colored species from Guatemala and Honduras is known only in the female sex. The females of *crocina* can be readily distinguished from any other Central American species

(including Mexico) of *Eumelissodes* by the sharply pointed pygidial plate, the ferrugineous mesoscutal hairs, the densely punctate interband zone of tergum 2, and the shiny galeae. It seems to be related to the *microsticta* group of North America, specifically to *M. micheneri*.

Female. Measurements and ratios: N, 3; length, about 11 mm.; width, about 4 mm.; wing length, M = 2.83 ± 0.200 mm.; hooks in hamulus, M = 12.33 ± 0.880; flagellar segment 1/segment 2, M = 1.82 ± 0.032.

Structure and color: Integumental color as in *microsticta* except as follows: clypeus with apicomedian area rufescent (holotype) or black; basitibiae and tibiae often rufescent (holotype); tegulae rufescent.

Structure and sculpture as in *microsticta* except as follows: clypeus with apicomedian carina distinct, about two-thirds as long as clypeus, punctures large, shallow, irregular laterally and apically; supraclypeal area dulled by reticular shagreening; lateral areas vertex with punctures more distinct, separated mostly by half to one puncture width or slightly more, surface shiny; galeae shiny above, unshagreened; maxillary palpal ratio about 3.3:2.0:2.0:1.0; mesoscutum with small impunctate posteromedian area, posterior to impunctate area punctures crowded, elsewhere separated mostly by half to one puncture width or slightly more; metasomal tergum 1 with punctures of basal three-fifths shallow; tergum 2 with basal area punctures large, round, deep, separated mostly by half a puncture width, surface shiny, interband zone punctures same size as those of basal area, very regular in size and spacing, separated mostly by half a puncture width or slightly more, surface dulled by coarse reticular shagreening, apical area with minute punctures separated by two to four puncture widths, surface moderately dulled by fine reticulotransverse shagreening; tergum 3 similar to 2 but interband zone punctures smaller, apical area punctures more crowded, apical area restricted; pygidial plate V-shaped, apex acute.

Hair: Head white to pale ochraceous except abundant brown on vertex. Mesepisterna with ventral and lower-anterior surfaces brown, lower-lateral surfaces white to pale ochraceous, upper-lateral surfaces orange-red; metepisterna and propodeum white to pale ochraceous; scutellum brown medially, fringed with yellow or orange; mesoscutum with brown posteromedian patch equal to about twice scutellar dark area (holotype) or less, anteriorly and laterally dark ochraceous to bright orange-red; tegulae without

brown. Metasomal vestiture as in *microsticta* except as follows: tergum 2 with interband zone hairs appressed to subappressed, distal pale band may reach apex of tergum at extreme sides (holotype); tergum 3 like 2 but basal tomentum dark brown, distal pale band reaches apex in lateral fourths or less (not in holotype); tergum 4 with apical area absent or reduced to short broad medial apical triangular area (holotype); terga 5 and 6 dark brown, with few or no pale lateral hairs; sternal hairs brown, paler laterally. Legs as in *microsticta* except as follows: middle tarsi and outer surfaces fore and middle tibiae brown; inner surfaces hind basitarsi reddish brown; scopal hairs yellow, may be washed with brown medially (holotype) from basitibial plate to tip of tibiae, basitarsal scopal hairs at least half dark brown.

Type Material. The female holotype was taken at San Cristobál, Guatemala, in January. One female paratype was collected February-March, 1931, at Santa Emilia (Pochuta), Guatemala, by J. Becquaert. One female paratype was collected September 20, 1917, at Teguecigalpa, Honduras, by F. J. Dyer. The holotype is in the American Museum of Natural History, New York City. The paratypes are in the collections of the Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, and the U. S. National Museum, Washington, D. C.

NOMINA DUBIA

The six names listed below are here considered to be *nomina dubia* since, so far as the author has been able to determine, the types of each have been lost or destroyed. Furthermore, the author has been unable to identify these species from the original descriptions which are too brief and without sufficient detail or figures.

Melissodes americana (Lepeletier), 1841, Hist. Nat. Ins. Hym., vol. 2, p. 92 (as *Macrocera americana*) (Carolina, Illinois).

Melissodes cajennensis (Lepeletier), 1841, Hist. Nat. Ins. Hym., vol. 2, p. 94 (as *Macrocera cajennensis*) (French Guiana).

Melissodes pennsylvanica (Lepeletier), 1841, Hist. Nat. Ins. Hym., vol. 2, p. 97 (as *Macrocera pennsylvanica*) (Pennsylvania).

Melissodes philadelphica (Lepeletier), 1841, Hist. Nat. Ins. Hym., vol. 2, p. 97 (as *Macrocera philadelphica*) (Pennsylvania).

Melissodes atriventris Smith, 1854, Cat. Hym. British Museum, vol. 2, p. 310 (North America).

Melissodes intermedia Cresson, 1872, Trans. American Ent. Soc., vol. 4, p. 278 (Texas).

ADDENDA

The following notes pertain to species or subgenera described in the previously published parts of this revision (LaBerge, 1956).

Melissodes (Melissodes) colliciata Cockerell

Melissodes colliciata Cockerell, 1910, Ann. Mag. Nat. Hist., ser. 8, vol. 5, p. 257.

Melissodes elusa LaBerge, 1956, Univ. Kansas Sci. Bull., vol. 47, part 2, p. 1061 (new synonymy).

Since the publication of the description of *M. elusa*, the author has had the opportunity of examining the holotype and cotype males of *M. colliciata* Cockerell which are in the collection of the Zoologische Museum der Humboldt Universität, Berlin (East), Germany. They are without doubt the same species and the name *elusa* must go into synonymy.

Melissodes (Ecplectica) haitiensis, n. sp.

This is a second species of the subgenus *Ecplectica* from the West Indies which brings the number of species belonging to this subgenus in the area covered by this revision to three. *M. haitiensis* is known from a single female, but is so distinctive as to merit recognition at this time. In the key to species (Laberge, 1956, p. 1041) of *Ecplectica* and *Melissodes s. str.* (the species of these two subgenera being in the same key), *haitiensis* does not fall with the other two species of *Ecplectica*, but goes to *M. tessellata* (couplet 10, p. 1043) which it resembles closely. *M. haitiensis* can be readily distinguished from *tessellata* by the lack of the distal pale pubescent band of tergum 2 and by the hyaline, yellowish apical areas of terga 1 to 4. This last character plus the densely tessellate and opaque surfaces of the head, mesoscutum, scutellum and mesepisterna will separate *haitiensis* from all other species of the subgenera *Ecplectica* and *Melissodes*.

Female. Measurements and ratios: N, 1; length, about 13 mm.; width, about 4 mm.; wing length, 3.27 mm.; hooks in hamulus, 16; flagellar segment 1/segment 2, 2.28.

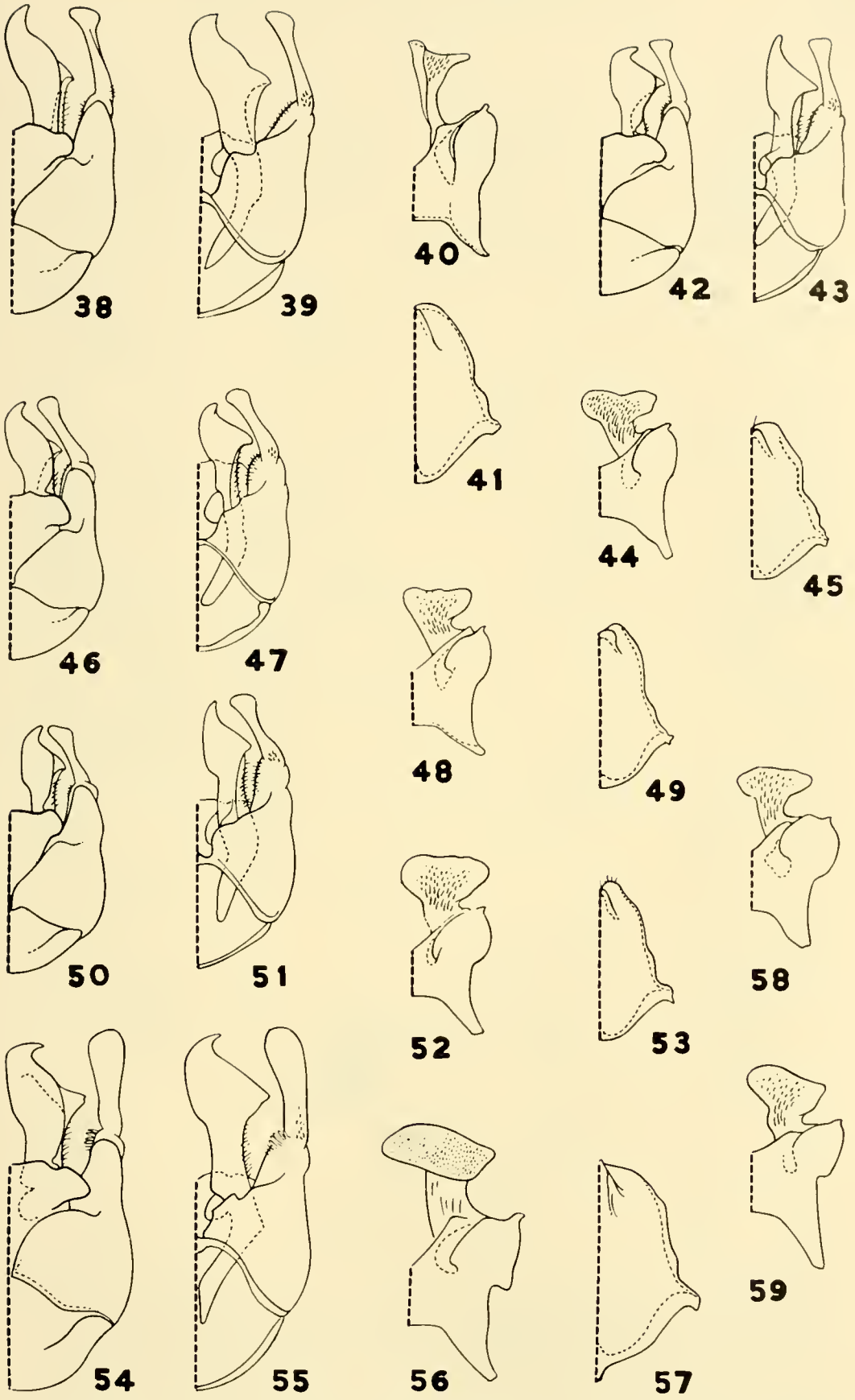
Structure and color: Integumental color black except as follows: mandibles, distitarsi, sterna rufescent; flagellar segments 3-10 and apex of 2 yellow below; eyes gray-brown; wing membranes slightly infumate, yellowish brown, veins dark brown; tegulae testaceous; tibial spurs white; terga 1-4 with apical areas hyaline, yellowish, shaded to brown posteriorly.

Clypeus flat, oculoclypeal distance less than half minimum width first flagellar segment, with small, shallow, round punctures, surface dulled by dense tessellation; supraclypeal area dulled by dense

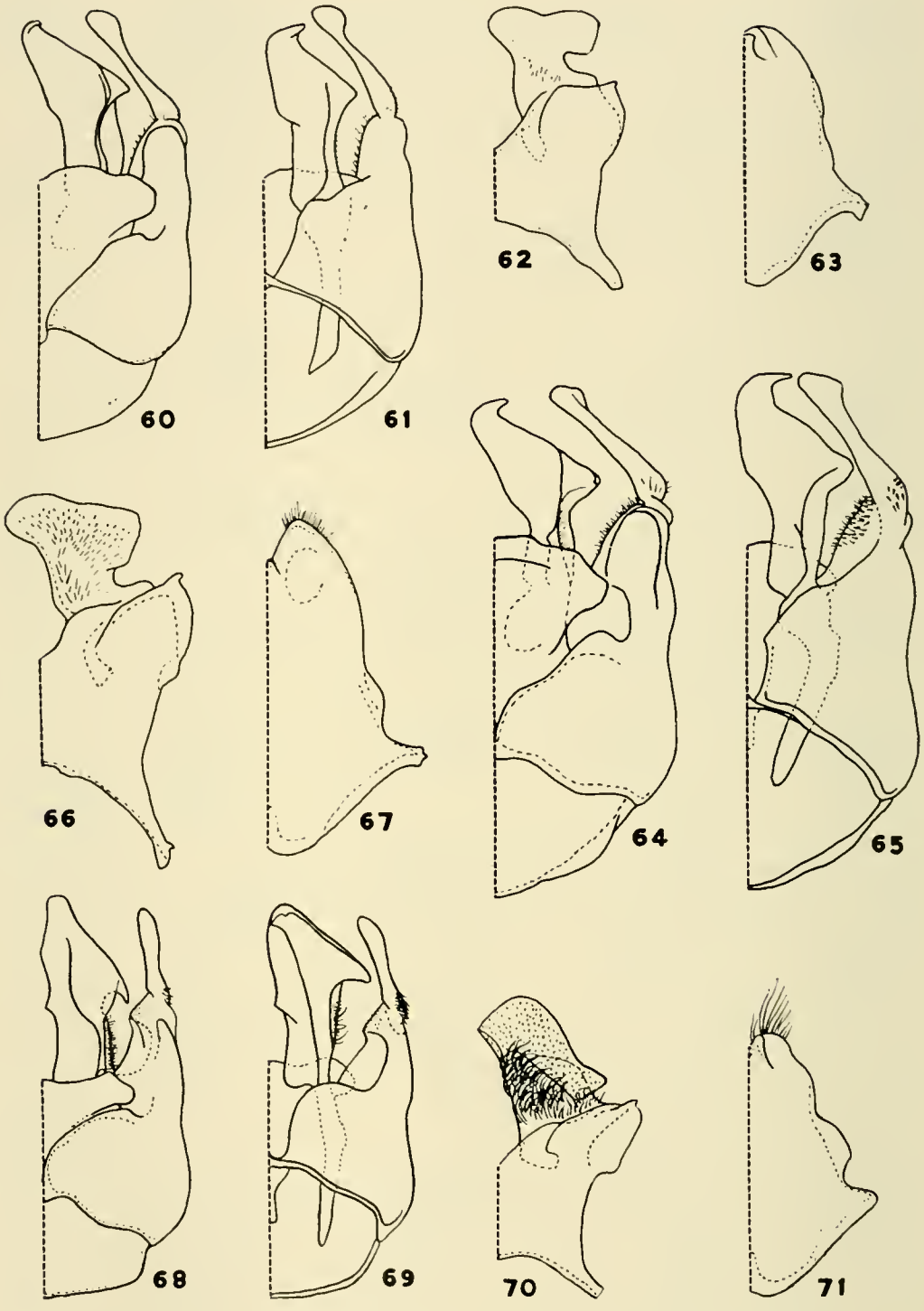
tessellation; vertex with lateral areas with minute punctures separated by two to three puncture widths, opaque, tessellate; galeae above shiny, unshagreened; maxillary palpal ratio about 1.6:1.5:1.5:1.0. Mesoscutum with round shallow punctures separated by half to one puncture width peripherally and one to two puncture widths posteromedially; scutellar punctures slightly smaller and more crowded; mesepisternal punctures like peripheral mesoscutal punctures; thorax everywhere opaque, surfaces (and bottoms of punctures) dulled by dense regular tessellation. Metasomal tergum 1 with basal three-fifths with extremely shallow punctures separated mostly by one to two puncture widths, apically impunctate, surface opaque, dulled by fine, but extremely dense, reticulotransverse shagreening; tergum 2 with basal area punctures small, round, separated mostly by half a puncture width, surface shiny, interband zone with round punctures slightly larger than in basal area, separated by half a puncture width, surface opaque as in tergum 1, apical area with small punctures separated mostly by three to four puncture widths, surface dulled by fine reticulotransverse shagreening; terga 3 and 4 similar to 2 but interband zone punctures denser and apical area absent on fourth; pygidial plate V-shaped, longer than broad, rounded apically; gradulus of tergum 6 with lateral parts absent.

Hair: Head white with abundant brown on vertex. Thorax white laterally and posteriorly; scutellum dark brown fringed with white; mesoscutum ochraceous with posteromedian dark brown patch more than twice size of scutellar dark area; tegulae without brown. Metasomal tergum 1 pale ochraceous basally, with long subappressed simple brown hairs fringing posterior margin of glabrous apical area; tergum 2 white basally, interband zone and apical area with abundant, appressed to subappressed, simple, dark brown hairs, distal pale band absent; tergum 3 with basal tomentum dark brown, distal pale band present, of ochraceous pubescence, subequal to apical area in length medially, and not reaching apical margin at sides, interband and apical areas as in tergum 2; tergum 4 like 3 but pale pubescent band apical with small apicomedial triangular area with suberect brown hairs; terga 5 and 6 dark brown, sparse pale lateral hairs on fifth; sterna dark brown except white laterally. Legs white except as follows: inner surfaces tarsi bright golden yellow; outer-apical surfaces fore and middle tibiae and basitibial plates brown.

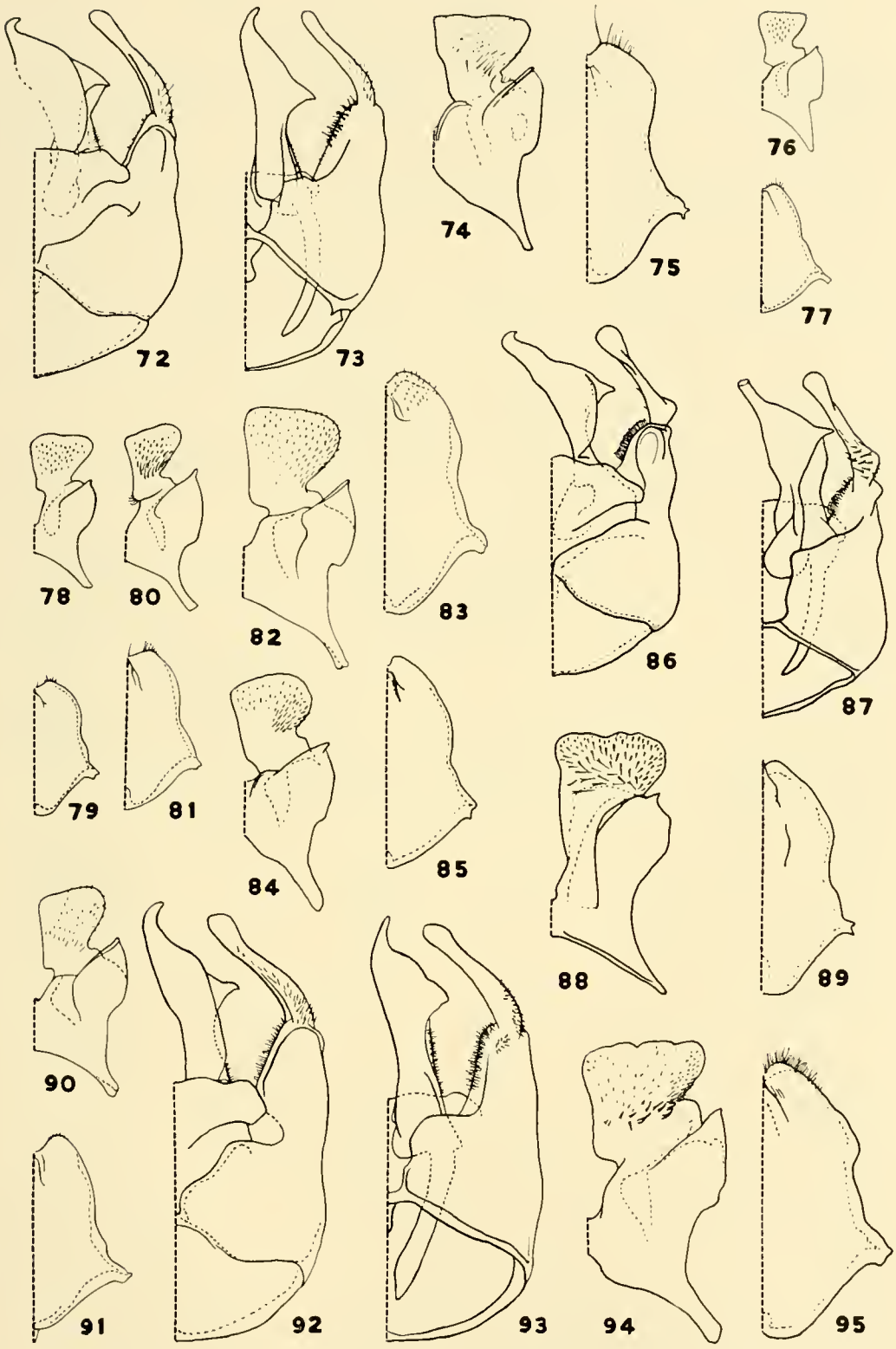
Type Material. The holotype female was collected April 8, 1922, at Carrefour, Haiti, and is in the collection of the American Museum of Natural History, New York City.



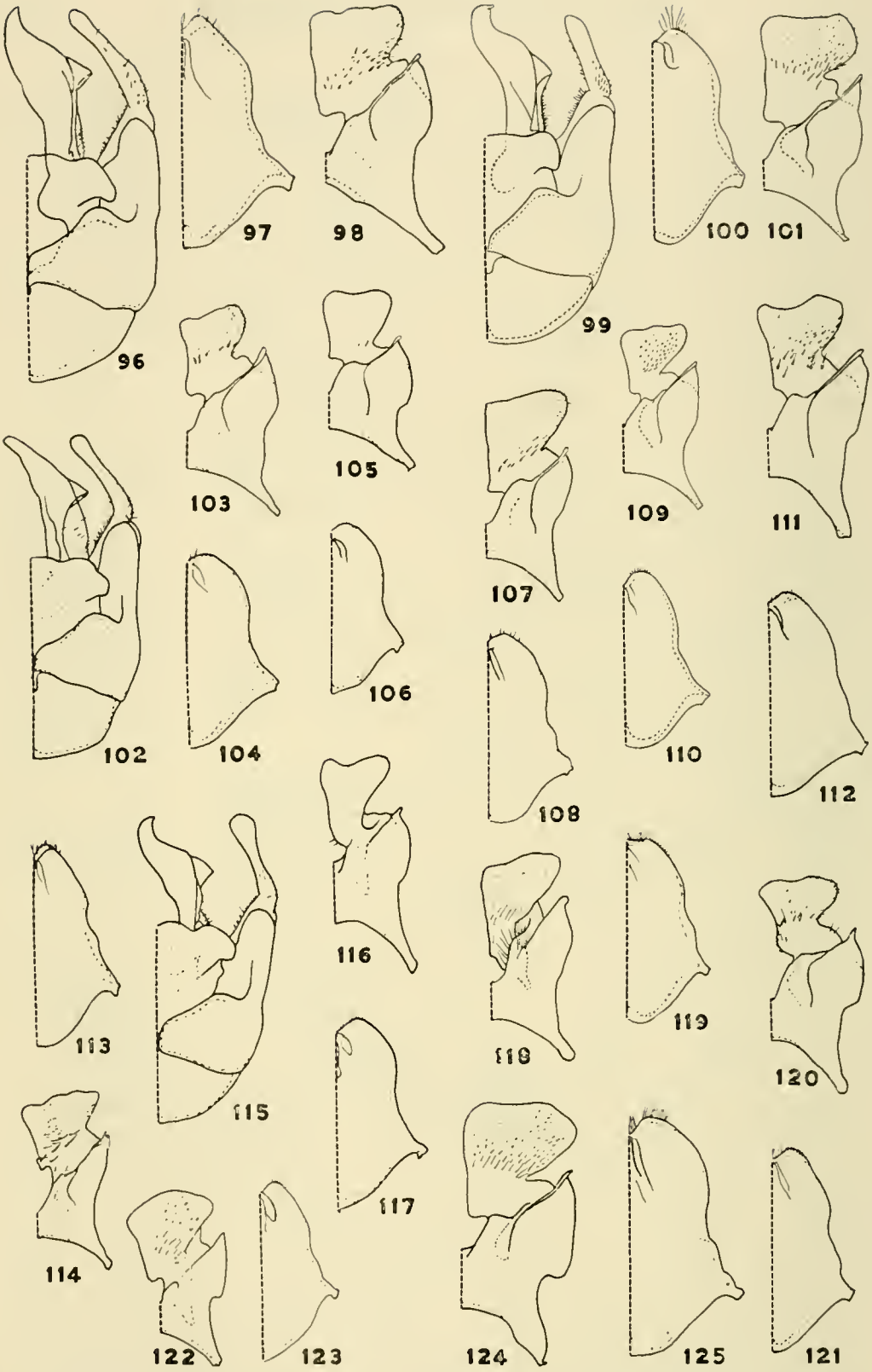
FIGS. 38-59. Male terminalia, approximately × 29. Subgenus *Callimelissodes*. 38-57. Genital capsules (dorsal and ventral views) and sterna 7 and 8 (ventral views) as follows: 38-41. *M. lupina*. 42-45. *M. plumosa*. 46-49. *M. metenua*. 50-53. *M. clarkiae*. 54-57. *M. nigracauda*. 58. Sternum 7 of *M. composita*. 59. Sternum 7 of *M. lustra*.



FIGS. 60-71. Male terminalia, approximately × 36. Subgenus *Callimelissodes*. Genital capsule (dorsal and ventral views) and sterna 7 and 8 (ventral view). 60-63. *M. glenwoodensis*. 64-67. *M. coloradensis*. 68-71. *M. stearnsi*.



FIGS. 72-95. Male terminalia, 76-81 and 90-91 approximately × 17.5, all others approximately × 36. Subgenus *Eumelissodes*. When four figures are indicated they are genital capsule (dorsal and ventral views) and sterna 7 and 8 (ventral views); if two figures are indicated, they are sterna 7 and 8. 72-75. *M. agilis*. 76-77. *M. trinodis*. 78-79. *M. bidentis*. 80-81. *M. dentiventris*. 82-83. *M. snowii*. 84-85. *M. boltoniae*. 86-89. *M. tristis*. 90-91. *M. fumosa*. 92-95. *M. vernoniae*.



Figs. 96-125. Male terminalia, approximately × 31. Subgenus *Eumelissodes*. When three figures are indicated they are genital capsule (dorsal view) and sterna 7 and 8 (ventral views); if two figures are indicated, they are sterna 7 and 8. 96-98. *M. pallidisignata*. 99-101. *M. subillata*. 102-104. *M. subagilis*. 105-106. *M. humilior*. 107-108. *M. verbesinarum*. 109-110. *M. utahensis*. 111-112. *M. brevipyga*. 113-114. *M. vernalis*. 115-117. *M. microsticta*. 118-119. *M. paulula*. 120-121. *M. personatella*. 122-123. *M. melanura*. 124-125. *M. moorei*.

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Those names now known to be synonyms, homonyms, or *nomina dubia* are marked with asterisks.

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The Crane Fly Genus *Dolichopeza* in North America

BY

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* This work was done primarily while the author was in the Division of Insects, University of Michigan Museum of Zoology, Ann Arbor, Michigan.

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INTRODUCTION

A hundred years have passed since Charles Darwin, in *Origin of Species*, wrote: "As the species of the same genus usually have, though by no means invariably, much similarity in habits and constitution, and always in structure, the struggle will generally be more severe between them, if they come into competition with each other, than between the species of distinct genera." During that century, repeated observations on various groups of organisms—vertebrate and invertebrate animals, as well as plants—have supported Darwin's belief, and these observations have been summarized in statements known as Jordan's Law and, more recently, Gause's Principle. Closely related species and races will by reason of their common origin inhabit ranges in proximity to each other. Competition between these species in areas where their ranges overlap is calculated to result in the survival of one and destruction or displacement of the others. The consequences of such competition are described in a statement of Jordan's Law by Hubbell (1936: 518-519): "In any group of allied forms, whether species or races, the most closely allied will be found not in the same territory and habitat, nor in widely separated regions, but either in adjacent areas separated by a barrier of some sort, or if in the same area then in different but not entirely unrelated or dissimilar ecological situations."

Because this expectation is so completely reasonable, instances of nonconformity with it are of unusual interest. Such an instance is found in the crane fly genus *Dolichopeza,* it having been the experience of collectors that wherever they took one species of the genus they nearly always collected at least one other. In fact, at

one time, in a certain favorable habitat, I captured no less than six species of *Dolichopeza* in a single sweep of my net!

As organisms usually conform to our well-founded generalizations, one tends to regard the case of *Dolichopeza* with suspicion. If we have interpreted the genus correctly, its species must be reasonably closely related; the fact is that certain groups among North American *Dolichopeza* comprise pairs or larger aggregations of sibling species, the forms so nearly alike that they may be distinguished only by microscopic details, in many cases. But it might be that the species are ecologically separated in some way as to preclude competition. Or, in view of the existence of groups of sympatric "sibling species," perhaps many of the recognized forms are really not species at all but merely polymorphic phenotypes of one or a few species.

The following study was undertaken partly to try to learn which of the described forms actually are species. This required extensive laboratory rearing, field observation and detailed study and interpretation of variation. It was the further purpose of this investigation to find how the species are related to each other, structurally and ecologically. This involved some study of comparative anatomy of both adults and immature stages, and again detailed field observations. Lastly, an answer was sought to the question: if there are closely related species living together in the same habitat, as has appeared to be the situation, how is it that one has not eliminated the others through competition?

Earlier North American workers on the Tipulidae have quite naturally concentrated their efforts on exploration of the fauna, which is still not completely known, even on the basis of the adult flies. Because of the relatively minor economic importance of crane flies, there has been no pressing need for studies of their biology; accordingly, the few earlier detailed accounts of North American tipulids have dealt usually with only one species or a scattering of species within a large genus. The following study, in contrast, attempts to present a more coherent picture, bringing together all available data on every species of the genus *Dolichopeza* known to occur in North America.

In gathering these data, it soon became evident that nearly every aspect of the biology of *Dolichopeza* was either uncertain or unknown. Geographical ranges were only sketchily outlined, only fragmentary information was available on the immature stages of but a single species, nothing was known of the internal morphology

of either adults or immatures, and the habitats of these stages had not been specifically defined. This investigation therefore expanded into a search for whatever could be learned about the genus *Dolichopeza*, with the idea that answers to the problems posed above might be found in diverse places.

ACKNOWLEDGMENTS

If I were to place a note of dedication in the front of this work, that dedication would be to the late Professor J. Speed Rogers, former Director of the University of Michigan Museum of Zoology, for it was Dr. Rogers who encouraged me to undertake this study and who got me interested in crane flies in the first place. As a teacher, he was always enthusiastically interested in the progress of his students and ever ready with encouragement. He placed at my disposal his entire accumulation of *Dolichopeza*, a collection larger than all others in the world combined, but what was more important he impressed me with the desirability—in fact, the need—of supplementing laboratory observations by the study of living crane flies in their natural environments. He was a cautious and careful worker, maybe even meticulous, and he would not like to see a conclusion reached unless every available shred of evidence had been closely examined. While I cannot measure up to his ideals, it is my hope that the work which follows would have pleased him.

My sincerest thanks go to Professor Theodore H. Hubbell, now Director of the University of Michigan Museum of Zoology, for reading most of this paper in its early stages and offering many valuable suggestions, often in the form of thought-provoking questions. His advice and encouragement have been of immeasurable help.

Dr. Charles P. Alexander, distinguished student of the world fauna of Tipulidae, generously provided me with his collection records of *Dolichopeza* and allowed me to inspect, in his personal collection at Amherst, Massachusetts, the types and other specimens of North American and exotic species. I am indebted to Dr. Alexander for this invaluable aid and for his having constructed much of the foundation upon which this investigation is based.

For permission to do intensive collecting in various state parks in Indiana and for the courteous co-operation shown by park personnel, I wish to thank the Department of Conservation of the state of Indiana. Recognition is also due Dr. Irving Cantrall for per-

mission to do concentrated collecting on the University of Michigan's Edwin S. George Reserve.

Data on distribution and intraspecific variation have been considerably increased through the generous co-operation of several individuals and institutions. Dr. Joseph Bequaert made available types and other material in the Museum of Comparative Zoology at Harvard University; the collection of the United States National Museum was loaned by Dr. Alan Stone, and Dr. J. R. Vockeroth sent specimens from the National Museum of Canada. Others who made valuable contributions include Dr. Edward L. Kessel of the California Academy of Sciences, Dr. Jean Laffoon of Iowa State College, Mr. Peder Nielsen of Silkeborg, Denmark, Dr. E. F. Cook of the University of Minnesota, Dr. F. N. Young of Indiana University, Mr. J. A. Wilcox of the New York State Museum, Dr. W. V. Balduf of the University of Illinois; and the entomological staffs of the Illinois State Natural History Survey, the Academy of Natural Sciences of Philadelphia, the American Museum of Natural History, Pennsylvania State University, the Milwaukee Public Museum, and the University of Kansas, who generously allowed me to examine collections in those institutions during my visits there.

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THE GENUS *DOLICHOPEZA*

Including nearly a hundred and seventy recognized forms in nine subgenera, the genus *Dolichopeza* comprises a varied and extremely widespread assemblage of species, some of which are not markedly different from certain species of other tipuline genera. By reason of possible future changes in generic definition, species or even subgenera of the present-day genus *Dolichopeza* may eventually be assigned to other genera. The recognized subgenera, however, are clearly related and, in general, seem to be natural

groups of species. *Dolichopeza* includes those tipuline crane-flies which have extremely long legs and feet, the wing vein R_{1+2} ordinarily absent or atrophied, the rostral nasus small or lacking, and the radial sector of the wing usually short and nearly traverse. Certain of these characteristics, of course, are shared by other genera, and some are not true of all *Dolichopeza*. The major subgenera may be separated by characters set forth in a key by Alexander (1931b). They are: *Dolichopeza* Curtis, *Nesopeza* Alexander, *Mitopeza* Edwards, *Oropeza* Needham, *Trichodolichopeza* Alexander, and *Megistomastix* Alexander. In recent years, three additional subgenera, embracing only a few species, have been described by Alexander. These are: *Afrodolichopeza, Hovapeza,* and *Sinoropeza.*

Excepting South America and the Antarctic, all the major land masses of the world have some members of *Dolichopeza* in their insect faunas, and it may be that later exploration along the western highlands of South America will prove the genus to be also present there. The typical subgenus is the most widespread, represented by two species in North America, by four in Europe, five in Africa and Madagascar, eight in southern and eastern Asia, and thirty-five species in Australia and New Zealand. The only other subgenus bridging a major geographical gap is *Oropeza,* of which there are nine species known from eastern Asia (Japan, China, Korea, Formosa, and India) and thirteen from North America. Sixty-four species of *Nesopeza* are recognized, of which all are Asiatic and nearly all concentrated in southeastern Asia. There are ten species of *Trichodolichopeza* known from east-central to south Africa, and eight species of *Megistomastix,* found only in the West Indies. *Afrodolichopeza* includes a half-dozen species from east-central Africa; *Sinoropeza* comprises two species from southeastern Asia; and *Hovapeza* is known from a single species from Madagascar.

NORTH AMERICAN *DOLICHOPEZA*

This study is limited to the species of the subgenera *Dolichopeza* and *Oropeza* that occur upon the mainland of North America. Although few of the hundreds of species of Tipulidae inhabiting this continent are likely to be confused with *Dolichopeza,* it would be well, at the outset, to distinguish the genus from its nearer relatives. In having the terminal segment of the maxillary palpus very much elongated, the antennae with twelve or thirteen segments, the vein Sc_1 normally absent, and the cubitus with a deflected angle at cross-vein m-cu, *Dolichopeza* is included in the subfamily Tipulinae and

is excluded from the Limoniinae, some of which have a superficially similar general appearance. Among North American Tipulinae, only three genera have extremely long and slender legs, with the tarsus exceeding in length the femur and tibia together. Of these, *Brachypremna* and *Megistocera*, both of which are essentially southern in distribution, may at once be distinguished from *Dolichopeza* by their having a nasus on the rostrum, the vein R_{1+2} present, and the antennae quite short, approximately the length of the head. The species of *Tipula* and *Nephrotoma* that resemble *Dolichopeza* may likewise be separated by the presence of vein R_{1+2} and, in *Tipula*, by the obliqueness of the radial sector.

The wings of *Oropeza*, as of the Tipulinae generally, are characterized by the presence of the cell 1st M_2 (Fig. 1), while this cell is not found in the two North American species of the subgenus *Dolichopeza* (Fig. 2). The cross-vein m-cu joins the media beyond its fork in subgenus *Oropeza* but before the first fork of the media in *Dolichopeza*. Other lesser points of difference will be discussed later.

Immature stages of both subgenera of *Dolichopeza* closely resemble those of *Tipula*, although both larvae and pupae of *Oropeza* may be distinguished by the presence on the sides of the eighth abdominal segment of two blunt, conical lobes. I have not made any comparative study of the eggs of various tipuline genera. Detailed comparisons of the larvae and pupae of *Dolichopeza* with those of its nearer relatives will be made in the sections on the morphology of those stages.

There are at the present time sixteen species and one subspecies of North American *Dolichopeza* recognized in the literature. They are *Dolichopeza* (*Dolichopeza*) *americana* Needham, *D.* (*Oropeza*) *carolus* Alexander, *D.* (*O.*) *dakota* Alexander, *D.* (*O.*) *dorsalis* (Johnson), *D.* (*O.*) *dorsalis rogersi* (Alexander), *D.* (*O.*) *johnsonella* (Alexander), *D.* (*O.*) *obscura* (Johnson), *D.* (*O.*) *polita* (Johnson), *D.* (*O.*) *pratti* Alexander, *D.* (*O.*) *sayi* (Johnson), *D.* (*O.*) *sessilis* Alexander, *D.* (*O.*) *similis* (Johnson), *D.* (*O.*) *subalbipes* (Johnson), *D.* (*O.*) *subvenosa* Alexander, *D.* (*O.*) *tridenticulata* Alexander, *D.* (*O.*) *venosa* (Johnson), and *D.* (*O.*) *walleyi* (Alexander).

Of these, thirteen appear to be valid species: *americana, carolus, dorsalis, johnsonella, obscura, polita, sayi, similis, subalbipes, subvenosa, tridenticulata, venosa* and *walleyi*. I consider *Dolichopeza pratti* to be a subspecies of *polita*, *dakota* a synonym of *walleyi*, and

sessilis and *dorsalis rogersi* synonyms of *dorsalis*. Support for the opinions expressed here will be found in the treatments of the individual species involved. One new species in the subgenus *Dolichopeza* and a new species and one additional race of *polita* in *Oropeza* are described and named in this revision.

In addition to the venational distinction between the subgenera mentioned earlier, a further convenient division of the genus may be made on the basis of the gonapophyses of the male hypopygium (Fig. 3). As the male of the one new species of subgenus *Dolichopeza* is unknown, *D. americana* is in a class by itself, in this regard. Five of the other species have the gonopophyses in the form of small knobs, densely covered at the tip by stout, black, curved spines. This group includes *johnsonella, obscura, polita, subalbipes,* and *tridenticulata,* and one new species; it will be referred to hereinafter as the *obscura* group. In the remaining species, the gonopophyses are generally flattened and blade-like, variously tipped, and without the abundant black spines of the *obscura* group. These constitute the *sayi* group, which includes *carolus, dorsalis, sayi, similis, subvenosa, venosa* and *walleyi.* Gonapophyses of representative species of these groups are compared in figures 4 through 7.

The genus may also be subdivided into two major color groupings: those species that are of a dusky brown coloration (*americana, johnsonella, obscura, polita,* and *tridenticulata*) and those which are chiefly yellowish or buffy and marked with darker spots and stripes, especially in the form of prescutal stripes and pleural spots on the thorax and dark annulations on the abdomen. The darkly colored species are most often found associated with deep shade, in either rock-gorge or wooded situations, while the paler forms are more characteristic of less intensely shaded, often sparsely sun-flecked vegetation. These circumstances, of course, invite speculation about the selective advantage of coloration in *Dolichopeza.*

HISTORICAL REVIEW

The genus *Dolichopeza* was established by John Curtis in 1825 to include the one known European species, which he named *Dolichopeza sylvicola* (Curtis, 1825: Plate 62.)* This species had already been described as *Tipula albipes* by Ström in 1768.

* Curtis' *British Entomology* is a series of colored plates, 770 in all, accompanied by descriptive notes. Published in London, these plates were issued a few each month from 1823 to 1840.

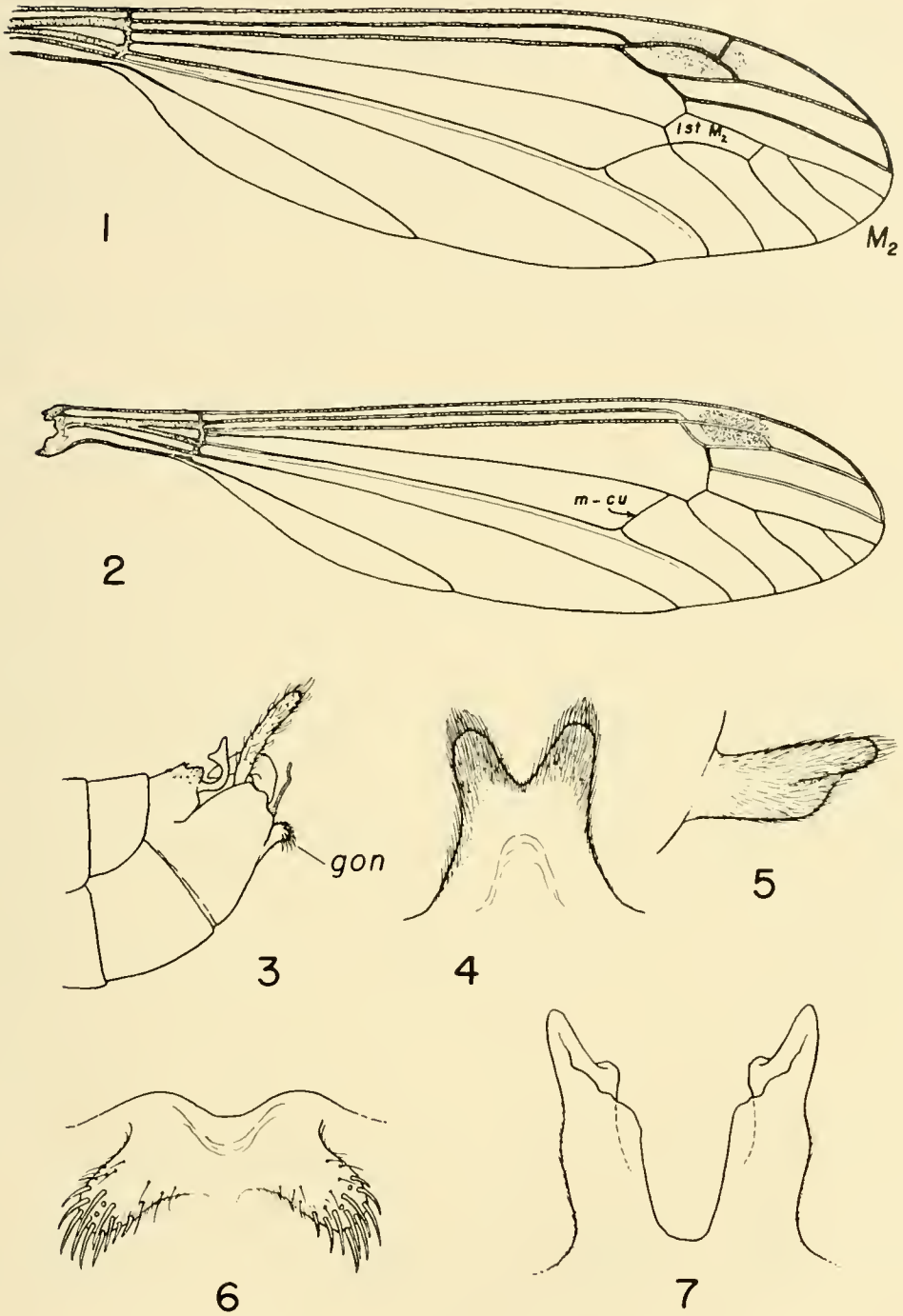


FIG. 1. Wing of *Dolichopeza (Oropeza) tridenticulata,* showing cell 1st M_2 or discal cell. FIG. 2. Wing of *Dolichopeza (Dolichopeza) americana,* showing position of m-cu cross-vein relative to first branching of M. FIG. 3. Hypopygium of *Dolichopeza (Oropeza) obscura,* male, left lateral aspect; gon—gonapophysis. FIG. 4. Gonapophyses of *Dolichopeza (Dolichopeza) americana,* dorsal aspect. FIG. 5. Same as 4, left lateral aspect. FIG. 6. Gonapophyses of *Dolichopeza (Oropeza) obscura,* postero-ventral aspect. FIG. 7. Gonapophyses of *Dolichopeza (Oropeza) sayi,* postero-ventral aspect.

Accordingly, the type species is *Dolichopeza albipes* (Ström). America's great pioneer entomologist, Thomas Say, in 1823 described *Tipula annulata* (Say, 1823: 25), the description of which is now thought to pertain to a species of *Dolichopeza.* Unable to locate the specimens upon which Say based his description, I must assume any types were lost at the time most of the Say collection was destroyed by dermestid beetles, in Philadelphia, about 1840 (Weiss and Ziegler, 1931: 203-212.)

Actually, it is uncertain that what Say described was a *Dolichopeza;* the description is quite brief and rather general in its wording. However, sometime between 1823 and 1828, specimens thought to be *Tipula annulata* Say reached C. R. W. Wiedemann in Austria, and in 1828 he noted that both male and female of this species were represented in his collection (Wiedemann, 1828:54). I have examined these specimens (now in the Naturhistorisches Museum in Vienna), which are two males and a female of *Dolichopeza* (*Oropeza*) *johnsonella* and two males of a species of *Tipula.* That these were determined by Wiedemann (they are so labelled) suggests they had not been compared with any specimens in America but were merely identified by comparison with Say's written description of *Tipula annulata.*

Fifty years later, C. R. Osten Sacken (1878: 40) placed *Tipula annulata* provisionally in *Dolichopeza,* noting that ". . . the forceps of the male has a different structure, etc." Seven specimens of *Dolichopeza* spp., labelled "*Dolichopeza annulata* Say?" (probably in Osten Sacken's handwriting) are to be found in a tray marked "Loew and Osten Sacken" in the Museum of Comparative Zoology at Harvard University. Osten Sacken's catalogue indicates that specimens of what he called *Dolichopeza annulata* were located in that museum. It would appear that Osten Sacken, like Wiedemann, decided after reading Say's description that certain North American tipulids in his collection were the species in question. It was Osten Sacken, however, who first critically compared North American *Dolichopeza* with *Tipula.*

Dr. James G. Needham, in 1908, described a new species, *Dolichopeza americana,* which he recognized as a true *Dolichopeza,* and also established the genus *Oropeza* to include a structurally similar American species in which the cell 1st M_2 is present in the wing. It seems that Needham, too, made an independent decision as to the identity of Say's *Tipula annulata,* for after having collected certain specimens which he so identified, he made *Tipula annulata* the type species of *Oropeza.* It was not long after Needham's work

that the actual diversity of North American *Dolichopeza* became known, through the investigations of Mr. Charles W. Johnson of Boston. In his "New and Little Known Tipulidae," published in 1909, Johnson described seven new forms and redescribed *Oropeza annulata*, assigning it the name *Oropeza sayi*. (Say had not been aware that Linnaeus had, in 1758, given the name *Tipula annulata* to the crane fly now known as *Limonia annulata*.) Johnson recognized as new species: *Oropeza similis, O. dorsalis, O. venosa, O. albipes, O. subalbipes,* and *O. obscura,* and a form *polita* as a variety of *obscura*. The individual histories of these, as well as of the other species listed in this summary, are treated under their separate titles.

All rearrangements and descriptions of species of North American *Dolichopeza* published since Johnson's paper have been the work of Dr. Charles P. Alexander. Arranged chronologically, they are: 1922—*Oropeza rogersi;* 1930—*Oropeza johnsonella;* 1931—*Oropeza walleyi* described and Johnson's variety *polita* raised to full species rank; 1931—the genera *Oropeza* Needham and *Dolichopeza* Curtis merged, together with other genera, into the genus *Dolichopeza,** as subgenera (Alexander, 1931b: 269); 1931—*Dolichopeza* (*O.*) *tridenticulata;* 1940—*Dolichopeza* (*O.*) *subvenosa;* 1941—*Dolichopeza* (*O.*) *pratti* and *D.* (*O.*) *sessilis;* 1942—*Dolichopeza* (*O.*) *albipes* renamed *D.* (*O.*) *carolus,* since, through his action of 1931, he had made *Oropeza albipes* Johnson a homonym of *Dolichopeza albipes* (Ström), of Europe; 1942—*Dolichopeza* (*O.*) *rogersi* reduced to subspecific rank; and 1944—*Dolichopeza* (*O.*) *dakota* described.

The biology of North American *Dolichopeza* has been given brief treatment by Alexander in "The Crane Flies of New York" (Part I, 1919; Part II, 1920); and the late Dr. J. Speed Rogers has made several additions to the knowledge of the biology of adult and immature stages in his studies of the Tipulidae of the Cumberland Plateau (Rogers, 1930), of northern Florida (Rogers, 1933), and of the Edwin S. George Reserve, Michigan (Rogers, 1942).

MATERIALS STUDIED

Over 11,300 adult and 600 later stage immature specimens of North American *Dolichopeza* have been examined in the course

* Johnson (1910:708) had earlier indicated this relationship of the two groups by using the heading "*Oropeza* Needham (*Dolichopeza* Curtis)" above a list of species of *Oropeza*. However, in a later paper (Johnson, 1925:32), he used the name *Dolichopeza americana* and the generic name *Oropeza* for several other species.

of this study. Adult flies were distributed among the various species as follows:

americana—1016
carolus—1150
dorsalis—285
johnsonella—425
obscura—2028
polita sspp.—2150
sayi—257
similis—67
subalbipes—530
subvenosa—138
tridenticulata—2617
venosa—132
walleyi—558
new spp.—31

Eggs of all species have been examined, and first instar larvae were obtained in all instances except *subalbipes, subvenosa, tridenticulata* and the two new species. Later instar larvae were obtained for all species except *carolus, johnsonella, subvenosa* and the new species referred to above; and pupae were found for all but *johnsonella* and the new species.

Of the total number of adults, about 2900 were in the Rogers collection at the University of Michigan, and somewhat over 600 were seen in collections from other individuals and institutions. More than 7800 adults and all but a dozen or so of the immature stages were collected during my field trips in the summers of 1949-1953 and 1957-1958. The types of all species were examined, except *americana* and *sayi*, of which species all type material is lost.

In the study of the natural history of *Dolichopeza*, many hundreds of samples of mosses and hepatics, representing perhaps 200 species, were collected and examined for larvae or pupae. Most of these contained neither, but abundant sampling was necessary, since all bryophytes were suspected habitats, especially at the outset of the search. Many actual habitats certainly would have been overlooked had any other procedure been adopted.

Incidental observations on and collections of plants and animals ecologically related to *Dolichopeza* were made. These observations have been interpreted and the collections identified by various specialists whose contributions are mentioned separately later.

COLLECTION AND PREPARATION OF MATERIAL FOR STUDY

Species of *Dolichopeza* vary in their response to light but are generally negatively phototropic, seeking the deep shade beneath undercut rocks and banks or the green twilight below lush vegetation of marsh borders and swampwoods. Unlike the more active and rapidly flying species of *Tipula* and *Nephrotoma* found in the same general habitats, *Dolichopeza* spends the daylight hours in shaded seclusion and must be hunted in somewhat the way a mammalogist might search for bats in the daytime.

Aggregations of individuals numbering from a few to over 200 may be found in cool, shaded niches in the more favorable forest and ravine habitats. In such cases, many flies may be collected by a single sweep of the net, or the patient collector desiring mating pairs or undamaged specimens may take flies directly into the cyanide jar. Under such conditions, I have collected mating pairs into large, empty jars in order to obtain eggs or observe mating behavior. For flies resting among the roots of wind-thrown trees or in narrow crevices in rock, collection directly into cyanide vials may be the best method, although an alternative is to stir within the cranny with a branch, collecting the flies into the net as they move out.

In collecting those species of *Dolichopeza* which are most frequently associated with vegetation of marsh borders and swamps (especially *D. dorsalis* and *D. sayi*), the usual "sweeping" technique is not satisfactory, as it is likely to break the legs off these delicately built crane flies. Rapid trampling of the vegetation will often bring the flies up from their hiding places. In doing this, one should look well ahead, especially for flies crossing small open spaces in the vegetation as they move ahead of the collector. Standing quietly in one place, or moving very slowly, has also proved a profitable method for detecting the movements of these crane flies beneath the cover of plants, and so capturing them. *Dolichopeza sayi, D. similis* and *D. dorsalis* are seldom seen in concentrations and must be taken individually or a few at a time. Other swamp species may be found either dispersed as individuals or gathered into small groups, where some sort of darkened cavity occurs. *Dolichopeza carolus,* usually seen hanging from leafy vegetation in forested ravine habitats, is easily taken by an upward sweep of the net.

To most entomologists, the words "crane flies" at once suggest the legless condition in which these insects are all too often found in collections. That the Tipulidae are fragile certainly cannot be denied, but proper handling will prevent undue loss of legs from most specimens. Correct preparation of specimens begins with their capture. Large cyanide jars are to be avoided; use of smaller vials (30 x 90 mm. shell vials, taped for reinforcement, are very good) prevents breakage of specimens because fewer are placed in one vial, and they have less room to shake around, during and after the killing process. Very shortly after a crane fly is killed in the cyanide vial, it becomes more fragile than when alive. It remains in this rigid but not brittle condition for two to three hours, after which there occurs a period of secondary relaxation, lasting somewhat over an hour. Following this period, dehydration causes

increasing brittleness of the insects. To attempt to disentangle and further prepare specimens either during the earlier period of rigidity or after dehydration has become advanced results in great loss of legs, especially in such slender-legged flies as *Dolichopeza* and many species of *Limonia*. During the period of secondary relaxation, however, even the most fragile species may be processed with some speed and without much damage. The flies are placed in paper envelopes (a convenient size is 2 x 3½ inches, No. 2 drug type), upon which the collection data have previously been marked. While still in the relaxed condition, three or four *Dolichopeza*, each with the long legs compactly arranged beneath the body, may be neatly tucked into such an envelope. Warm, dry heat or a calcium chloride desiccator may be used to dry the insects. Specimens prepared in this way arrive in the laboratory undamaged, ready to mount, and accompanied by field data.

Most breakage of tipulids in collections is due to improper mounting. I have never seen a crane fly too large to be conveniently mounted on a point of heavy paper. Flies pressed in envelopes are arranged in one plane, hence are seldom broken during the mounting or labelling processes. Utilization of points cut from two-ply bristol-board for all mounting allows the use of uniformly strong pins (No. 4 are good) and thus prevents damage of specimens due both to attempts to pin through the insect's body and to subsequent pin failure. Dried with the legs folded below the body, flies may be fastened to the point by the left side of the thorax, in such a way that only the one side of the thorax is obscured from view, while the legs receive maximum protection from the point, the pin, and the labels. China cement thinned with ethyl acetate is a very satisfactory mounting material.

In the preparation of labels, the guiding principle should be to make all essential information about the specimen immediately available to other workers who may wish to make use of it, be they in another part of the world or in a different generation or century. Adequate locality data consist of first a major geographical division (state, province, territory, or country, if of small size), then a more limiting designation, a county, district, or reference to a sizeable town, etc., such as is likely to be listed in the indexes to commonly accessible maps. Geographic co-ordinates should be used for little-known areas. References to any but the most widely-known physiographic features is inadequate, as these may not be mentioned in atlases or map indexes. Elevations should always be given for regions of high relief, and specific localities should be

mentioned for areas where other environmental factors (vegetation, moisture, etc.) vary greatly. Exact dates are very important, especially in data on groups such as the Tipulidae that are very seasonal in occurrence. Special material (reared specimens, those from which parts have been removed to microscope slides, etc.) should be appropriately labelled. Confusion is certain to occur, sooner or later, if identified insects are not *each* labelled with the proper determination, the authority and the date.

Collection of larvae and pupae is a tedious and time-consuming business, for the immature stages are usually diffusely distributed within their microhabitats. It is practically impossible to obtain eggs or first instar larvae by field collecting methods. About two months after the local peak of late-summer emergence of adults is a good time to gather larvae, if numbers are desired, for the larvae will have grown large enough to be readily seen but will not have been seriously reduced in numbers by predators or severe weather. I believe that predation on the young of the spring generation progresses more rapidly and that the *Dolichopeza* population is thus more quickly reduced.

If fewer individuals but higher percentages of emergence are desired, larvae or pupae should be gathered shortly before the local time for emergence under natural conditions. Most natural mortality will then have occurred, and, given reasonable care in the laboratory, nearly all larvae or pupae will go on to the adult stage. Some hints on the actual places to look for larvae may be found in the discussion of larval habitats. However, an observation of general application is that additional pupae and perhaps larvae are likely to be found in mosses from which pupal skins are projecting, provided that these sites are discovered early in the season of emergence for the species concerned.

Immature stages to be preserved are killed in hot water and stored in 80% alcohol. I have not found it necessary to pass specimens through increasing concentrations of alcohol before storage. Adults stored in alcohol tend to lose their color, although color patterns are often accentuated in the process. Soft structures, both internal and external, retain their shape and are more easily studied in alcoholic material. Large collections of flies may be stored in a small space, in alcohol, although extensive damage to individual specimens will eventually occur, during subsequent handling.

Microscopic preparations used in this study were very simply made. Most materials were soaked in 80% alcohol or warm water until soft, or were first macerated to the desired degree in 7-10%

potassium hydroxide solution and then rinsed in warm water, then transferred directly into polyvinyl alcohol mounting medium.* This substance has good optical qualities, is very inexpensive, and has a slight clearing action that makes the KOH treatment unnecessary in the case of smaller objects. A further advantage is that mounted specimens may be soaked off in hot water and remounted, in case slides become broken or mounts are unsatisfactory. Polyvinyl alcohol, or "PVA" as it is called, has been in use only about fifteen years, so its durability has not been proved.†

METHODS OF STUDY

Adults.—As in any study of a primarily taxonomic nature, this work is based largely upon post-mortem examination of museum specimens, in this case dried and alcohol-preserved flies. However, familiarity with and understanding of a group of organisms come more from studying them in their natural environment. Following insects about to learn what they are up to may seem an idle occupation, in these times when laboratory biology is more the vogue, but particularly in studies involving several closely related, sympatric species, such as is the case with *Dolichopeza*, field observations lead to a better understanding of individual species and may provide the only answers to certain problems of inter-species relationships. Large numbers of living flies were also caged in the laboratory for such purposes as obtaining eggs, observing mating behavior, noting approximate length of life, and other things that could not easily be studied in the natural habitats.

Contraction or deflection of parts of the body in drying, or distention in alcohol, cause inaccuracies and complications in both linear and proportional measurement. For purposes of general description, body length, as used hereinafter, means the straight-line distance from the most anterior part of the head (excluding antennae) to the tip of the abdomen, regardless of the position in which the specimen is preserved. Wing length, the most fixed and easily accessible measurement of adult *Dolichopeza*, is the straight-line distance between the point of attachment and the tip. Even wing length is of little use in describing species, for environmental factors may result in great differences in size within a species. Discussion of preserved adult crane-flies, therefore, will be concerned chiefly with structural characteristics.

* Polyvinyl alcohol is a plastic prepared from PVA powder (I use DuPont "Elvanol," grade 71-24): sift 20 grams of the powder into 88 cc. of cold water; heat at 85° F. in water bath, stirring constantly, until a viscous syrup forms; to 56 parts of this syrup, add 44 parts of a mixture of equal amounts of lactic acid and liquid phenol, stirring often and well.

† Dr. C. P. Alexander, who prefers Canada balsam, pointed out that, in the Baltic Amber, he has 30 or 40 million years' proof that balsam is a good mounting medium!

Larvae and pupae.—If larvae are taken in the late third or fourth instar, they will need little attention when brought into the laboratory. Rearing dishes must become neither too warm nor too dry; and, while the minimum lethal temperature is not known for any species, larvae were lost in considerable numbers at times when the room in which they were kept became warmed to temperatures that are only comfortable to humans. It has been stated that larvae of *Dolichopeza* inhabit dry moss. It is, however, difficult to estimate the actual moisture content of such a habitat, and the fact is that the larvae were usually found unable to survive one night in a covered dish containing no apparent moisture.

Rearing larvae from eggs is a difficult task, and my attempts to do this have not met with notable success. However, the following methods have been found workable. Adult females in breeding cages (wide-mouth, half-gallon canning jars were found adequate) will oviposit on moist pads of paper (commercial cleansing tissues were used) and sometimes on the sides of the jar. At the end of the laying period, these pads may be removed and the eggs concentrated upon a circular portion of the paper, such as will fit into a Syracuse dish, or the like. Eggs left in the jar may be removed by washing them down with water (at room temperature) and collecting them in a pipette or dropper. Heavier than water, they will collect in the tip of the pipette and may be transferred to the moist paper pad without overly wetting it. When the eggs are about five days old, fragments of moss should be placed beneath the paper, and the larvae, upon hatching, will migrate to this moss. Excessive moisture in the dish is to be avoided, for the eggs will not mature if submerged, and the very young larvae drown readily in even small amounts of free water beneath the paper. No more water should be in the dish than will be retained by the paper, but the dish should be kept damp by the use of a cover and the occasional replacement of evaporated moisture. Larvae feeding under the paper may be observed through the bottom of the inverted dish, to which the pad will adhere by its dampness.

As the larvae grow larger, increasing amounts of moss should be placed in the dish, but separated leaves and stems should still be used, in order that the activities of the larvae may be watched at any time and head capsules or cast skins may be recovered after each molt. When larvae have at last transformed into the fourth instar, moss clumps in their natural form may be used, for the last larval skin may be recovered from the pupal burrow, and the larvae are large enough to be located and observed easily.

After formation of the pupa, it becomes necessary to move specimens to a larger dish, so that there will be sufficient space for emergence of the adult. Unlike some other tipuline pupae, those of *Dolichopeza* are not very active and will usually remain in any artificial "burrow" that is arranged in the moss for them. It is, of course, possible to bring larvae through all instars and pupation in a large dish, such as is recommended for pupae, but observation is very difficult and recovery of molted skins is practically impossible under such conditions.

In order to avoid overheating larvae and pupae during microscopic examination, I have used a device containing an ordinary 150-watt electric lamp, with a water-filled Florence flask in front of it, serving both to absorb heat and condense the light into a very intense spot. While larvae are seldom found feeding in the light in their natural surroundings, they rapidly accommodate to the increased illumination of the laboratory and may continue eating even while being observed in the bright light of the microscope lamp.

For studying preserved immature stages, I have used a Stender dish about one-third filled with paraffin, into which were carved such shapes and sizes of holes as were necessary to hold the specimens still, under alcohol.

It might be appropriate to say a few things about laboratory culture of mosses. To begin with, it is advisable to keep a covered terrarium stocked with food mosses at all times during the rearing period, and to take from such stock supplies whatever moss is needed to maintain adequate food in the rearing dishes. Isolated cushions of moss tend to become dehydrated and overgrown with molds. When larger quantities of moss are grown together, normal nutrient substrate may be retained and the mosses grow more luxuriantly, while molds seem less able to gain a foothold. Varying the depth of damp sand beneath the terrarium mosses provides a moisture gradient, and mosses may be placed according to their natural water requirements. Mosses which begin to mold should be removed from the terrarium. It has been observed that molds are less likely to occur if the terrarium is kept in a cool, though lighted situation.

ADULTS—EXTERNAL MORPHOLOGY

General description.—Smaller than most of the Tipulinae and larger than the average of genera of the Limoniinae, *Dolichopeza* is medium sized, as crane flies go. The body length from front of head to tip of abdomen varies from about 7 to 15 mm., depending upon the species. Except in one species, *Dolichopeza polita* (all

its races), males average somewhat smaller in all dimensions than females. Wing length is approximately 8 to 15 mm. and again depends upon the species. Over-all size may vary not only with species but also with ecological fluctuations, as will later be explained in detail. Those characteristics which distinguish *Dolichopeza* from other tipuline genera have already been noted. The combined lengths of femur and tibia considerably exceed that of the wing, and the length of these two leg segments together is nearly always equalled or surpassed by that of the tarsus. The genus takes its name from this most striking feature; Greek *dolichos* = long, *peza* = foot. (*Oropeza* means "mountain-foot" and is derived from the Greek word *oros* = mountain.) This remarkable leg length, coupled with extreme slenderness, gives species of this genus a very characteristic appearance; it is what led one author to describe the legs of *Dolichopeza* as "excessively long."

Head.—Most of the surface of the head is occupied by the large, dichoptic compound eyes, which are of about equal size in both sexes and of a black color. There are no ocelli, which is characteristic of all Tipulidae. Surface areas of the head capsule proper, such as the occiput, vertex, front and genae, are poorly defined, but the clypeus is distinct, forming the upper (anterior) and lateral parts of the rostrum, or proboscis. There is no nasus on the rostrum in the North American species.

The antennae are composed of a rather cylindrical scape about four times as long as its width, a subspherical pedicel, and a flagellum of elongate, verticillate, more or less cylindrical segments, each somewhat thicker at the base than at the tip, and each beyond the first ordinarily shorter than the preceding segment (Fig. 10). In the subgenus *Dolichopeza,* there are ten flagellar segments (cf. Alexander, 1919:853), while in *Oropeza* there are eleven.

The rostrum bears the mouthparts, conspicuous among which are the two labellar lobes (apparently modified labial palps), each nearly covered on its oral surface by a system of pseudotracheae branching from two arcuate channels that convey liquid food to the tip of the hypopharynx, concealed beneath the heavily sclerotized, triangular labrum (Fig. 9). Peterson (1916:39) states that ". . . no piece is present at the base of any generalized palpus (of the Diptera) which can be homologized with the palpifer of generalized insects." He is supported in this opinion by Rees and Ferris (1939:146), Crampton (1942:34) and others. Accordingly, the basal portion of the maxillary palp (Fig. 8) is here interpreted not as a palpifer but as one of five segments, the terminal one

of which is longer than all the others combined, as in all Tipulinae. The maxillary palp attaches to a sclerotized structure which, although it is mostly internal, is here considered to be the stipes of the maxilla, on the basis of musculature (Fig. 9). The structure I interpret to be formed of the partially fused stipites has been called the "apodeme of the cranial flexor muscle of the lacinia" by Rees and Ferris (1939) and the "maxillary apodeme" by Crampton (1942).

Thorax.—In either dorsal or lateral aspect (Figs. 14, 15), the external thoracic surface is dominated by the sclerites of the mesothorax, which contains the flight muscles. Seen from above, the pronotum (pn) is a narrow, convex band, almost concealed beneath the prescutum, while the mesothoracic postnotum completely obscures the metanotum. Several clearly defined areas comprise the mesonotum; these are the prescutum (psc), medially divided scutum (sc), scutellum (scl) with a parascutellum (pasc) on each side, and a postscutellum (pscl), or postnotum. The term "thoracic dorsum," used in descriptive paragraphs of this paper, refers to the mesonotum, which sometimes bears conspicuous color markings, especially on the prescutum. The broadly V-shaped, complete transverse suture between prescutum and scutum is characteristic of the entire family Tipulidae. On each anterolateral margin of the prescutum is a shallow indentation, the pseudosuture or pseudosutural fovea (psf).

All three pleural sutures are distinct and the sclerites of the pleural region easy to identify (Fig. 14). There is, however, some difference of opinion as to what these sclerites should be called. Between the pronotum and anterior coxa is the prothoracic episternum. Just forward of this is a cervical sclerite, and along its posterior side is the small epimeron of the prothorax. The corresponding parts of the metathorax, located between the third coxa and the base of the haltere, are somewhat less clearly outlined. Extending from the second coxa to the base of the wing is the conspicuous pleural suture of the mesothorax. Immediately anterior to this is the mesepisternum, divided, sometimes indistinctly, into a dorsal anepisternum and a ventral pre-episternum (called sternopleurite by Alexander, 1942:199), which adjoins the coxa. Spots of dark color are found on these two areas, in certain species. Between the second and third coxae and rather closely applied to the former is the meron of the mesothorax (episternum, in Alexander, 1942:199), sometimes darkly marked. Above this is an irregularly shaped mesepimeron, or pteropleurite, which is

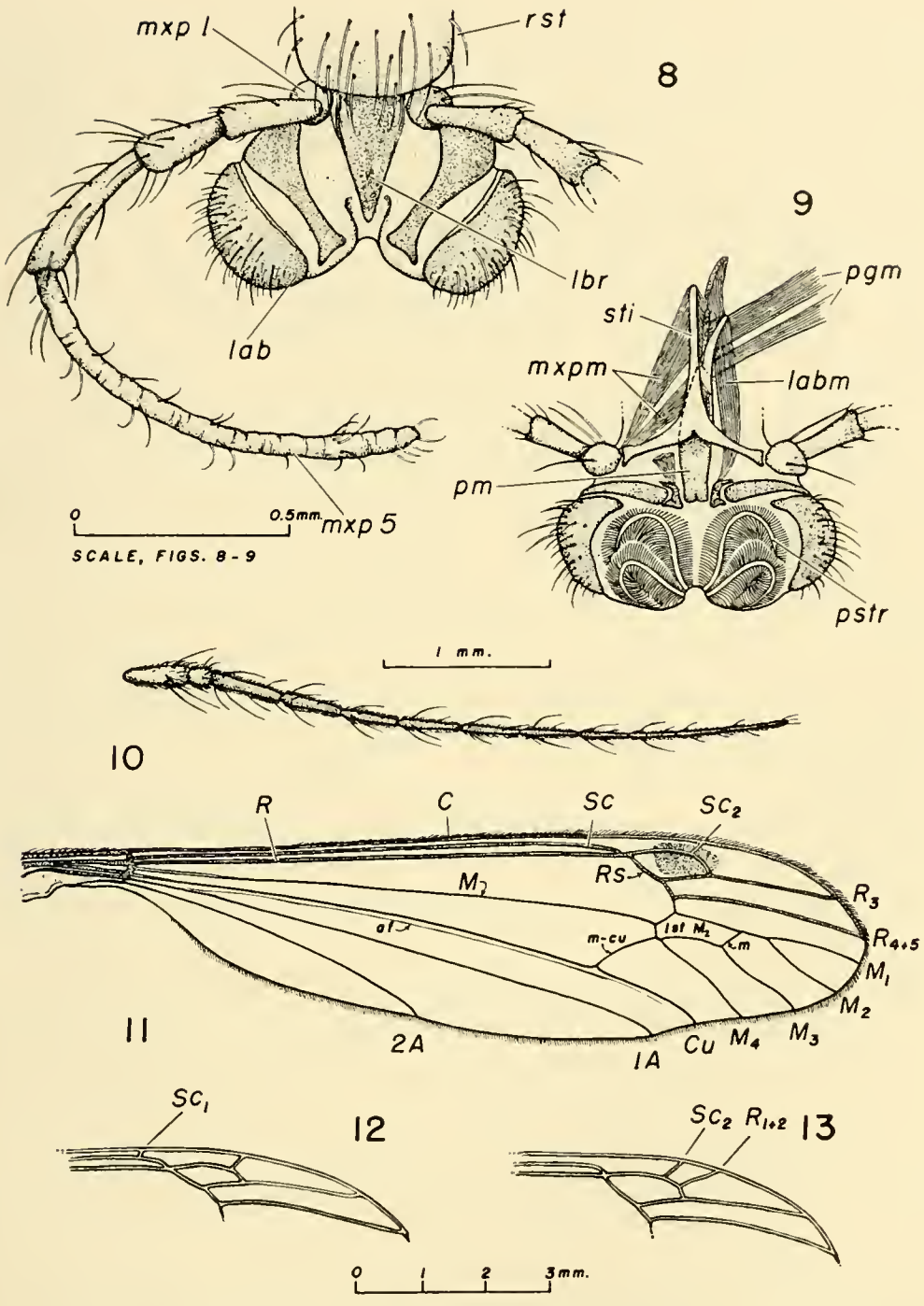


FIG. 8. Mouthparts of *Dolichopeza (Oropeza) polita*, antero-dorsal aspect; lab—labellar lobe, lbr—labrum, mxp 1—first segment of maxillary palp, mxp 5—fifth segment of maxillary palp, rst—rostrum. FIG. 9. Same as 8, postero-ventral aspect; labm—muscle of the labellar lobe (labial palp), mxpm—muscles of the maxillary palp, pgm—muscles originating on postgena and inserting on prementum, pm—prementum, pstr—pseudotrachea, sti—partially fused stipites. FIG. 10. Antenna of *Dolichopeza (Oropeza)* sp. FIG. 11. Wing of *Dolichopeza (Oropeza) carolus;* A—anal veins, af—anal fold, C—costa, Cu—cubitus, M—media, m—medial cross-vein, m-cu—median-cubital cross-vein, R—radius, Rs—radial sector, Sc—subcosta. FIG. 12. Wing of *Dolichopeza (Oropeza) carolus* showing the vein Sc_1 present. FIG. 13. Same as 12, showing the vein R_{1+2} present.

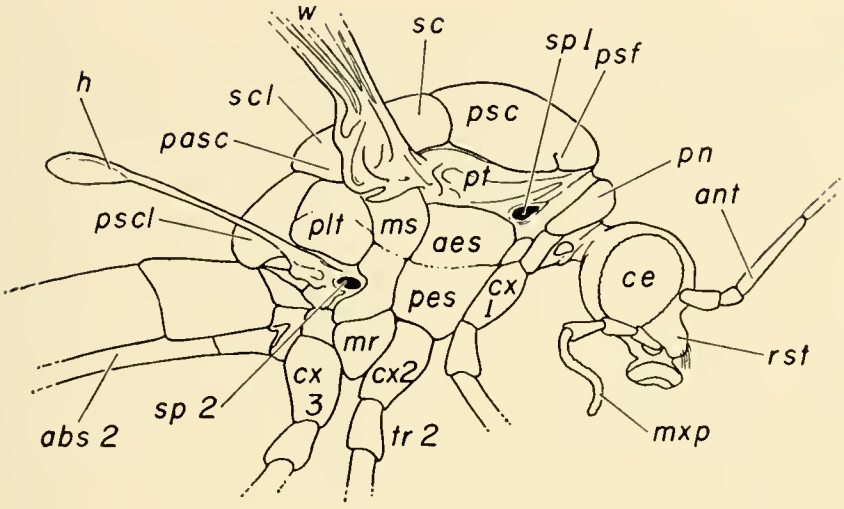
weakly divided into an anepimeron and katepimeron and is ordinarily unicolorous. Between the mesepimeron and the postscutellum lies a sclerite known as the pleurotergite, which Crampton (1942:49) states is actually a lateral division of the postscutellum. What I have called the postscutellum is referred to as the mediotergite of the postscutellum by Crampton.

The mesothoracic spiracle is situated in a membranous area at the anterior edge of the segment, between the anepisternum and prescutum, and the metathoracic spiracle lies just in front of the base of the haltere.

All species of *Dolichopeza* in North America have the wings unmarked except for narrow tinged bands along certain veins (especially the cubitus and m-cu cross-vein) and a weakly or strongly colored, brownish stigmal spot. Figure 11 illustrates the typical venation of subgenus *Oropeza*, in which the costa, subcosta and radius, including all its branches, are considerably heavier veins than any others. The humeral cross-vein is present, and the arculus is complete. Occasionally the vein Sc_1 is found in the position indicated in Figure 12, and rarely R_{1+2} is present (Fig. 13). Spurious cross-veins have occasionally been observed, especially between veins R_3 and R_{4+5}. As mentioned earlier, the cell 1st M_2 (discal cell) does not occur in the subgenus *Dolichopeza* (compare Figs. 1, 2). Designation of all veins follows the system used by Alexander (1942: 201).

Both the femora and tibiae are of a length about equal to that of the fly's abdomen, and the first segment of the tarsus alone is often longer than these two together. Each tarsal segment is of greater length than all those beyond it combined. The tibial spurs are slender and inconspicuous; they arise perpendicular to the axis of the tibia but bend sharply, so that the tip is nearly parallel to the tibia. The shape of these spurs seems to be the same in all species. Likewise, there is no apparent difference, from species to species, in the untoothed tarsal claws. Leg coloration aids in species identification, although any species may be properly identified by the use of other characters.

Male abdomen.—There are nine evident segments of the male abdomen (Fig. 16), the last of which, called the hypopygium, bears the genital appendages and other reproductive structures. The first and second terga are more or less fused, and the first sternum is shorter than the corresponding tergum. The third through eighth segments are unmodified. The tenth or anal segment (as) is represented by a membranous projection surrounding the end of the



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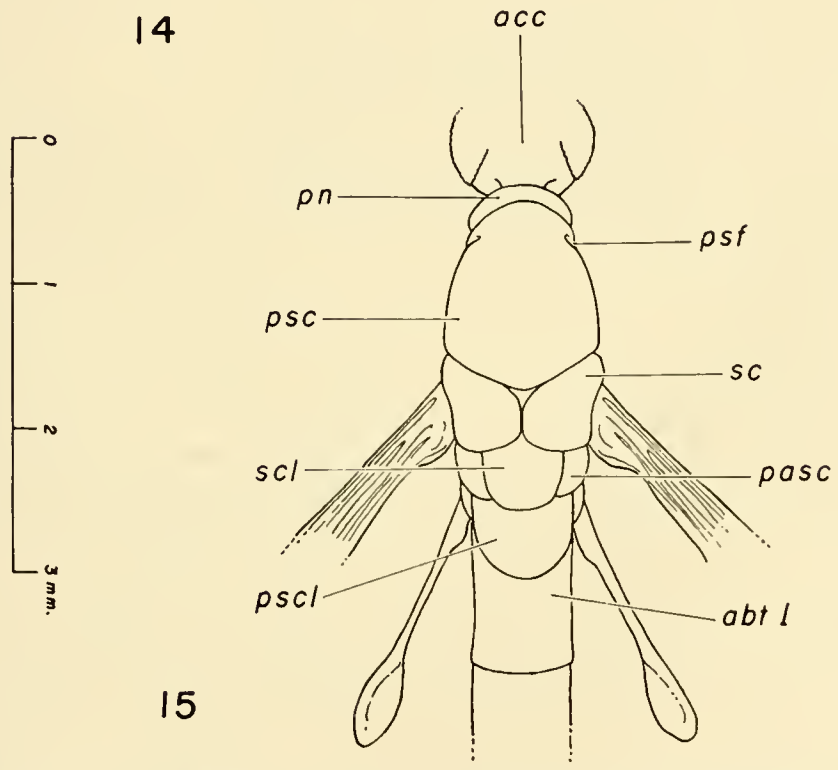

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FIG. 14. *Dolichopeza (Oropeza)* sp., right lateral aspect of thorax; abs—abdominal sternum, aes—anepisternum, ant—antenna, ce—compound eye, cx—coxa, h—haltere, mr—meron of mesothorax, ms—mesepimeron, mxp—maxillary palp, pasc—parascutellum, pes—pre-episternum of mesothorax, plt—pleurotergite, pn—pronotum, psc—prescutum, pscl—postscutellum, psf—pseudosutural fovea, pt—paratergite, rst—rostrum, scl—scutellum, sc—scutum, sp—spiracle, tr—trochanter, w—wing. FIG. 15. Same as 14, dorsal aspect; abt—abdominal tergum, occ—occiput, other abbreviations as in 14.

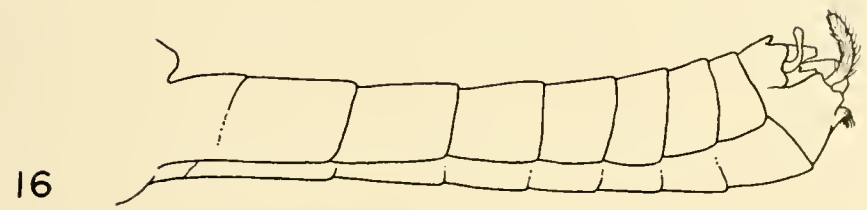
digestive tube and situated close beneath the middle of the ninth tergum.

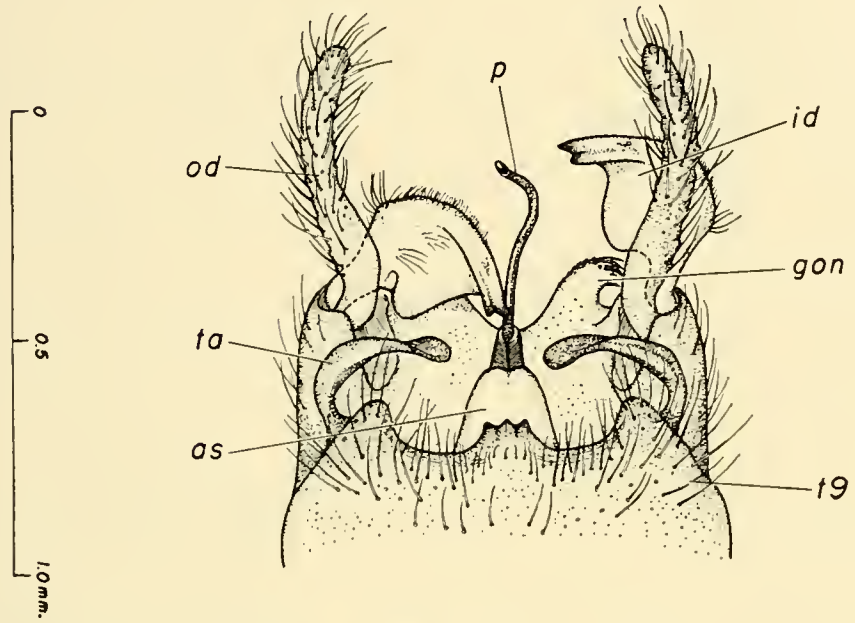
It seems probable that in primitive Diptera there were paired genital appendages, each comprising a basal and a distal segment, arising from the ninth abdominal segment in somewhat the arrangement found in existing Mecoptera—*Panorpa*, for example. These appendages appear to be highly developed lateral phallic lobes (Snodgrass, 1957: 44-47), although they have been widely regarded as modified abdominal limbs, or gonopods. In the Tipulinae, the basal portion (basimere, or coxite, of morphologists), which has been called the basistyle (Fig. 18, bs), is completely fused with the ninth sernum (s9). The distal portion (telomere, or stylus) in many crane flies has become divided into two separately articulated appendages (Fig. 17), a dorsal or outer dististyle (od) and a ventral or inner dististyle (id). The shapes of these structures can be used to a limited extent in classification.

The ninth tergum in the subgenus *Oropeza* bears heavily sclerotized lateral extensions, which may be called tergal arms (ta) and which function to brace the ventral valves of the female ovipositor during copulation. These have characteristic shapes, depending upon the species. While no such structures are found in the subgenus *Dolichopeza*, their absence is compensated by other parts of the hypopygium. I have been unable to learn any function of the various forms of the posterior margin of the ninth tergum, but it is a fortunate coincidence that this sclerite offers one of the most reliable means for species determination in males. It may be shallowly or deeply emarginate or crenulate, or may bear a median projection with sharp teeth or blunt lobes.

Between the basistyles, on either side of the midline of the ninth sternum, are the gonapophyses (gon), the various shapes of which have already been briefly discussed. The term "gonapophyses" has been used in many ways in the several orders of insects, but most authors agree that the gonapophyses of male insects are median projections in proximity to the gonopore. The origin and homology of the gonapophyses in *Dolichopeza* are unknown; Figure 29, however, indicates the close relationship between them and the adminiculum and basistyles. It seems advisable to retain the term for these particular structures since it does not appear to be misapplied.

The male intromittent organ, or penis (Fig. 17, p) is an extensible, slender and rather densely sclerotized tube, straight tipped, or nearly so, in some species and abruptly curved at the tip in others.





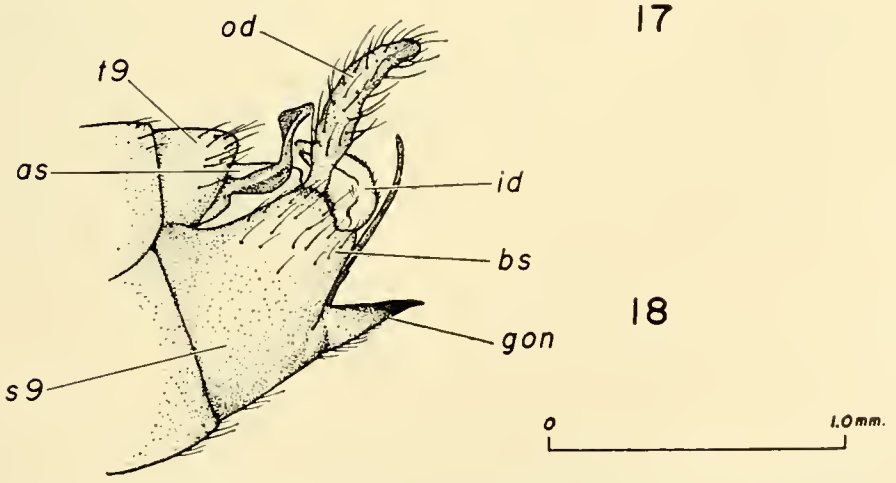


FIG. 16. Abdomen of male *Dolichopeza (Oropeza) tridenticulata*, left lateral aspect. FIG. 17. Hypopygium of male *Dolichopeza (Oropeza) tridenticulata*, dorsal aspect; as—anal (tenth) segment, gon—gonapophysis, id—inner dististyle, od—outer dististyle, p—penis, ta—tergal arm (lateral arm of ninth tergum), t9—ninth tergum. FIG. 18. Hypopygium of male *Dolichopeza (Oropeza) venosa*, left lateral aspect; bs—basistyle, s9—ninth sternum, other abbreviations as in 17.

Its method of extension will be explained later. Where the penis emerges from the floor of the genital chamber, it is braced by a cone-shaped, intensely sclerotized structure (Figs. 17, 28) that is actually formed from partial or complete fusion of two elements, one on either side. This has been termed the aedeagus by Alexander (1942, etc.) and the adminiculum by Mannheims (1951:10), Snodgrass (1957:45) and others. Its two component parts have been regarded as parameres (Tjeder, 1948), hypomeres (Rees and Ferris, 1939) and mesomeres (Snodgrass, 1957). These parts extend cephalad in the floor of the genital chamber and enter the abdominal cavity as short apodemes supporting the vesica (Figs. 28, 29). The term "aedeagus" has been used synonymously with what I have designated as the penis, also for the penis and its basal structures combined, and in other more restricted senses, almost always, however, as a phallic structure. Accordingly, I have adopted the term "adminiculum," meaning a support, for the function of this cone-shaped structure in *Dolichopeza* is strictly one of support and not intromission in any way.

Female abdomen.—There are ten clearly defined segments in the female abdomen, of which the eighth through tenth are modified to form the ovipositor (Fig. 19). As in the male, the first and second terga are somewhat fused, and the first sternum is shorter than the corresponding tergum. The third through seventh segments are unmodified. Small spiracles occur in the membranous pleura of the first seven segments but are usually concealed by overlap of the sclerites if most of the eggs have been laid. Except for the first, which has shifted to the forward edge of its segment, the spiracles are all near the midlength of their respective segments.

It has been argued by Crampton (1942:81) that the type of egg laying apparatus found in *Dolichopeza* and other crane flies ". . . should be referred to as an oviscapt, or ovicauda, rather than an 'ovipositor' . . . since its parts are not strictly homologous with those of a true ovipositor of the type occurring in orthopteroid insects." However, as the structure takes its name from its undeniable function of oviposition rather than from any homology, the term "ovipositor" is retained. In the typical pterygote ovipositor, the gonopore, opening between the eighth and ninth sterna, is flanked by a pair of blade-like valvulae, attached to basal sclerites (first valvifers) belonging to the eighth sternum, and two pairs of similar valvulae belonging to the ninth sternum. The latter pairs are attached to common bases (second valvifers) at either side, and

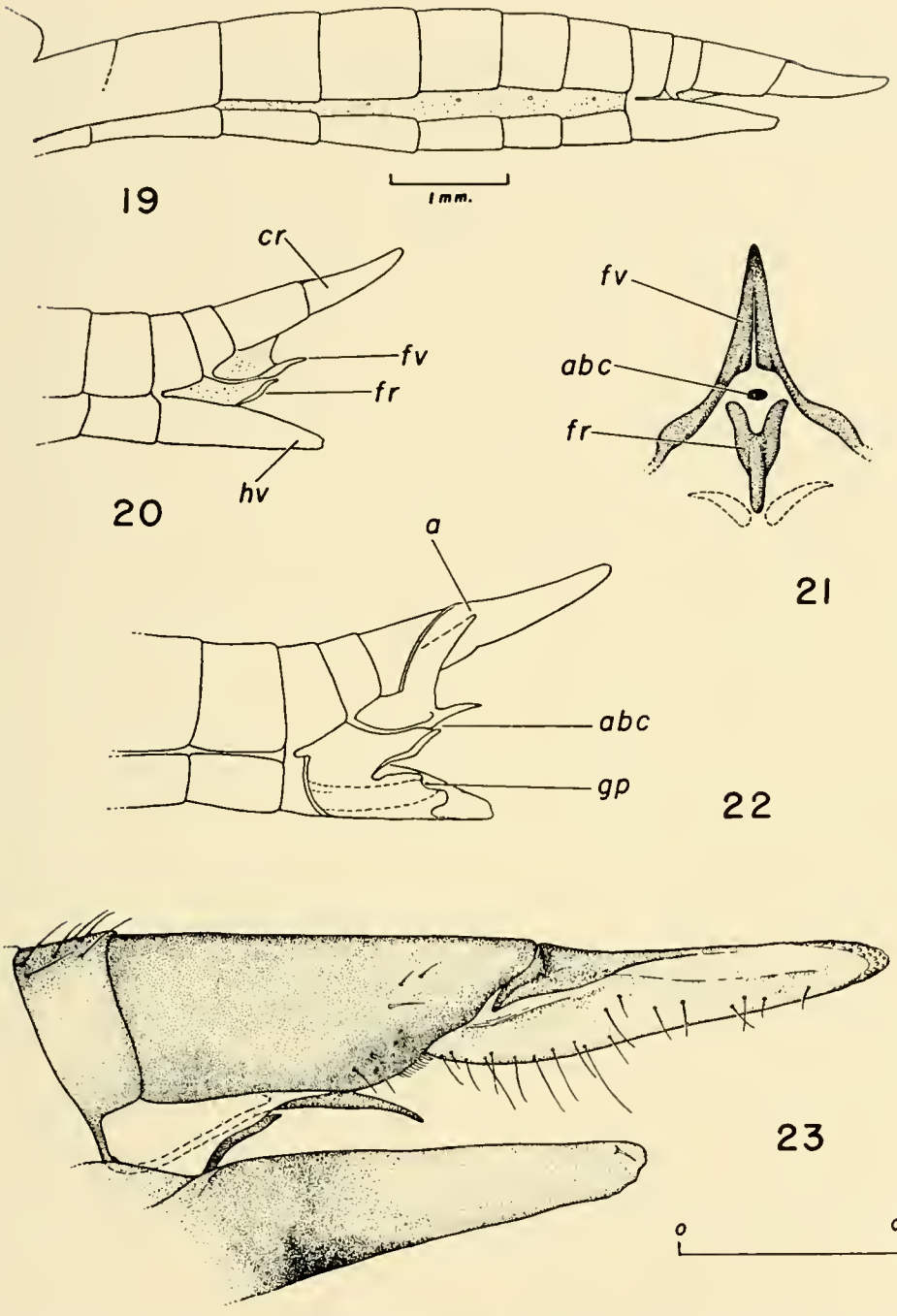


FIG. 19. Abdomen of female *Dolichopeza (Oropeza) tridenticulata*, left lateral aspect. FIG. 20. Same as 19, showing details of ovipositor; cr—cercus, fr—furca, fv—fused valvulae (ninth sternum), hv—hypovalve (extended eighth sternum). FIG. 21. Details of external reproductive structures of female *Dolichopeza (Oropeza) similis*, postero-ventral aspect; abc—aperture of bursa copulatrix, other abbreviations as in 20. FIG. 22. Details of reproductive structures of female *Dolichopeza (Oropeza) tridenticulata*, left lateral aspect, cut-away view; a—anus, abc—aperture of bursa copulatrix, gp—gonopore. FIG. 23. Ovipositor of female *Dolichopeza (Oropeza) johnsonella*, left lateral aspect, showing sensory structures.

all together comprise the ninth sternum. Snodgrass (1935:611) says of these, "The second valvifers usually retain a close connection with the tergum of the ninth segment, but the first valvifers are often more or less dissociated from the eighth segment." Above and to the rear of the typical ovipositor are the tenth and eleventh abdominal segments, with cerci arising from the membrane between them and with the anal opening situated close beneath the eleventh tergum.

The structure found in females of *Dolichopeza*, as in other tipulids, does not depart from this basic arrangement of parts except in details. Completely encircling the eighth abdominal segment at its anterior end is a rather strongly sclerotized ring which narrowly connects the tergum and sternum (Fig. 20). While the tergum is otherwise unmodified, the sternum is projected backward to beneath the tenth tergum, or further, in the form of a pair of egg guides, or hypovalves (hv), which however are fused nearly to their tips in the genus *Dolichopeza*. These hypovalves are pocketed on their inner surfaces to receive the tips of the inner dististyles of the male, in order to effect a firm attachment in copulation. Rising slightly from the inner floor of the hypovalves is the membranous end of the median or common oviduct, terminating in the gonopore (Fig. 22, gp). There is, in the narrow ninth segment, a modification of the sclerotized anterior ring found in the eighth. Semicircular above, where it corresponds to the anterior margin of the tergum, this band is, at the sides, deflected abruptly caudad and toward the midline, where its ends meet to form a fairly heavily sclerotized, triangular blade, which may be regarded as the fused second valvulae (Figs. 20, 21, fv), and thus the ninth sternum. Snodgrass (1903: 178) has called these the fused second gonapophyses. Between this reduced ninth sternum and the hypovalves, or eighth sternum, is the genital chamber. Immediately below the ninth sternum is the upper opening of the reproductive system, that which leads into what may be called the bursa copulatrix, since it is into this opening that the penis of the male is inserted in mating (Figs. 21, 22, abc). Thus, while it would seem that the two separate parts of the reproductive system open independently to the outside, it may be seen that both in fact enter the genital chamber as above defined.

Lying in the membrane beneath the aperture of the bursa copulatrix is a sclerotized fork, of which one tine extends to either side of the aperture. The base of this fork is in a pouch formed just above the oviduct (Fig. 22), and it sometimes happens that the

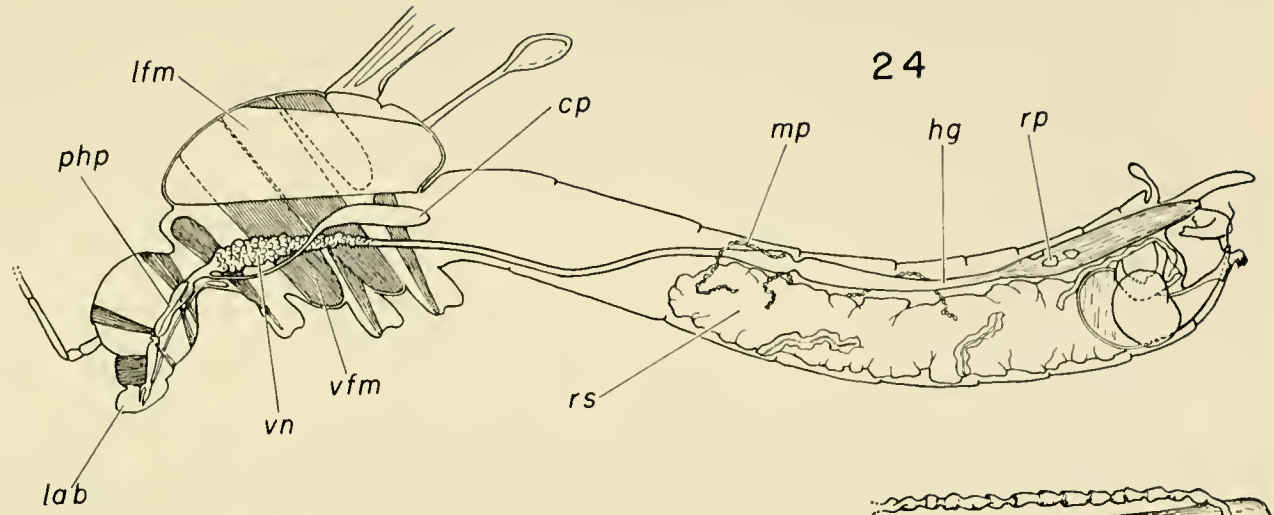
floor of this pouch (that is, the roof of the oviduct) bears small, usually weakly sclerotized areas, closely associated with the base of the fork, as indicated by the broken lines in Figure 21. Students of the Psychodidae (especially *Phlebotomus*) have called this fork the furca, the name that is adopted here (Figs. 20, 21, fr). Snodgrass (1903: 178) is of the opinion that the furca ". . . may be the fused and rudimentary anterior gonapophyses," by which he means the first valvulae and their valvifers in the sense used above.* This seems a sound interpretation in spite of the great modification of the parts involved.

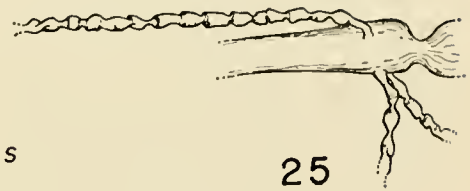
The tenth segment has a saddle-like and strongly sclerotized tergum (Fig. 23) but no sclerotized sternum. Beneath the posterior end of the tenth tergum is situated the anal opening. As in most crane flies, the cerci are strongly sclerotized and blade-like in shape, reinforced along their dorsal edges. Minute pegs grouped at the tips of the cerci (Fig. 23) are thought to be sensory in function, and it sometimes seems that females in the process of oviposition obtain impressions about the nature of the substrate by means of probing with the cerci. Inasmuch as the cerci have an important function also in the actual deposition of the eggs, they may be termed the dorsal (or "tergal") valves of the ovipositor. A small, indistinct sclerite between the bases of the cerci may be interpreted as the eleventh tergum.

ADULTS—INTERNAL MORPHOLOGY

Head.—Much of the interior of the head is occupied by portions of the central nervous system, particularly the brain and the large optic lobes, the convex apical surfaces of which are in contact with the basement membranes of the compound eyes. The only other conspicuous structures are the anterior parts of the digestive tube (Fig. 26). In the rostrum, the epipharynx (eph) and hypopharynx (hph) are fused basally, forming a partly sclerotized tube, the basipharynx (bph), which can be dilated by means of a thick muscle attached to its roof and originating on the anterior wall of the rostrum, or clypeus. Flexibly joined to the upper end of the basipharynx is the pharyngeal pump, a structure made up of three sclerotized elements connected by elastic membranes to form a tube that is somewhat expanded at each end and roughly triangular in cross section. Some authors have applied the term oesophageal pump to the pharyngeal pump. The arrangement of attached muscles suggests that dilation of the aboral end of the pharyngeal

* It is inadvertently stated by van Emden and Hennig (1956: 121) that Snodgrass homologized the hypovalves with the anterior gonapophyses.





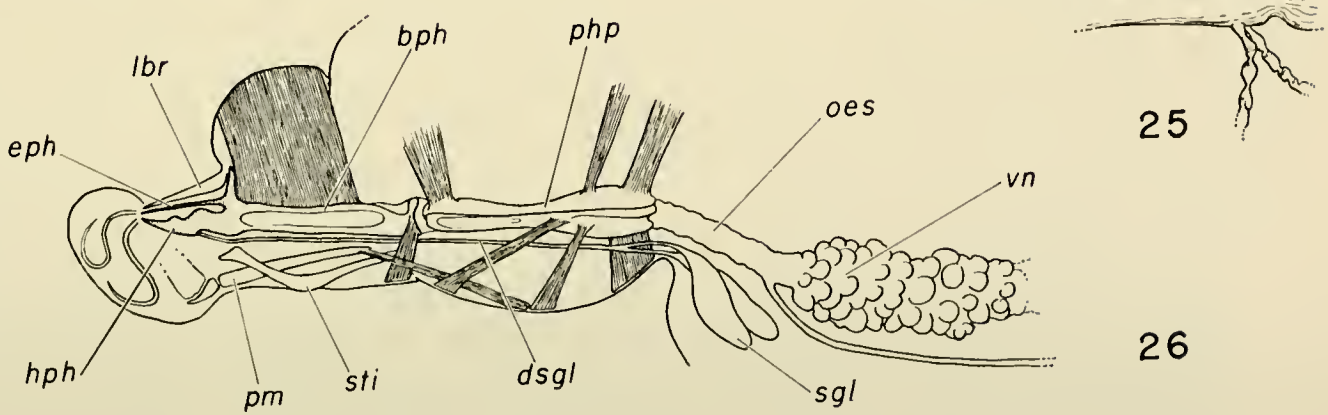


Fig. 24. Gross internal anatomy of adult male *Dolichopeza (Oropeza) tridenticulata;* cp—crop, hg—hind-gut, lab—labellar lobe, lfm—longitudinal flight muscle mass (shown as unshaded area superimposed over shaded vertical flight muscles), mp—Malpighian tubule, php—pharyngeal pump, rp—rectal papilla, rs—reproductive structures (shown as compact, intertwined mass heavily invested with adipose tissue), vfm—vertical flight muscles, vn—ventriculus. Fig. 25. Detail of digestive system of *Dolichopeza (Oropeza)* sp., showing appearance of Malpighian tubules in preserved specimen. Fig. 26. Details of digestive system, anterior portion; bph—basipharynx, dsgl—common duct of salivary glands, eph—epipharynx, hph—hypopharynx, lbr—labrum, oes—oesophagus, php—pharyngeal pump, pm—prementum, sgl—salivary glands, sti—stipes of maxilla, vn—ventriculus.

pump provides most of its action. A single salivary duct leads from the ventral side of the hypopharynx along the pharynx to the neck region, where the duct divides into two (Fig. 26). There is no tentorium.

Thorax.—By far the greatest volume of the thoracic cavity is taken up by the flight muscles: lateral, vertical bands and two large, longitudinal muscle masses, one on either side of the median plane, as outlined in Figure 24. A short length of membranous esophagus connects the oesophageal pump with the ventriculus in the cervical region. There appears to be no proventriculus. The anterior end of the ventriculus has a decidedly lumpy surface, the nodules being largest just behind the neck and diminishing in size until inconspicuous about midway through the thorax. A membranous crop, which with its duct-like proximal portion extends nearly the full length of the thorax, is attached ventrally at the junction of the oesophagus with the ventriculus (Fig. 26). Just within the thorax, beneath the oesophagus, lie the two small salivary glands, the ducts of which unite quite abruptly. The ventral nerve cord, passing through the thorax from the suboesophageal ganglion, produces three large thoracic ganglia, close below the digestive tube. These give off branches to the thoracic appendages and muscles.

Abdomen.—Except for varying amounts of fat tissue and the thin bands of muscles in the body wall, the contents of the abdomen consist almost entirely of the reproductive system and parts of the slender alimentary canal. Pale greenish gray and shining in a freshly killed fly, the reticulated fat tissue, most abundant in males, is dull white in specimens preserved in alcohol. The ventriculus, entering the abdomen along the floor of the first segment, curves up against the body wall to terminate dorsally in the third abdominal segment, at the point where the four Malpighian tubules attach. These excretory outgrowths are about as long as the entire body and are either coiled mostly in the upper part of the abdominal cavity or are intertwined among the other organs. In life, their color is mottled gray, but alcohol preservation usually renders them pale brown or reddish brown; also in life there may be a zone of yellowish coloration about the attachment of the Malpighian tubules. The hindgut is slightly enlarged at its anterior end, tapering evenly to the rectum, a thin walled and sac-like structure close beneath the seventh, eighth and ninth terga. Four irregularly oblong rectal pads (Snodgrass, 1935: 381) of opaque white color lie in the anterior part of the membranous rectal wall.

Male reproductive system.—A conspicuous arrangement of strongly sclerotized parts, lying primarily in the eighth and ninth abdominal segments, is visible in specimens cleared in KOH for mounting on microscope slides. These structures have been studied, variously named and employed in classification by many investigators (Snodgrass, 1904; Tokunaga, 1930; Edwards, 1938; Tjeder, 1948; Mannheims, 1951; Wood, 1952). As described earlier, each of the two elements forming the conical adminiculum is continuous with a flattened, sclerotized rod lying in the membranous floor of the genital chamber. Upon the anterior tips of these rods, which project into the abdominal cavity as apodemes, rests a bulb or capsule, which is joined to the base of the penis (Fig. 28). This has been called the spermatophore sac by Tokunaga, and the central vesicle by Snodgrass. Following the terminology used by Edwards (1938: 14), it is here called the vesica. As the vesica is capable of rotation in the sagittal plane, rocking on the tips of the adminicular rods, it is difficult to describe its parts as being dorsal or ventral, anterior or posterior, as can be done for those genera in which this organ is fixed in position. However when the penis is fully retracted, the vesica has the position indicated in Figure 28, and the following description is based upon the structure thus oriented. There are two wing-like outgrowths from the anterior surface of the vesica, one arising at either side of the base of the penis and curving down along the side of the bulb to about the point of flexible attachment of the vesica to the adminicular rods. These are the lateral apodemes (lap). From the posteroventral surface of the vesica extend two rather stout rods, diverging backward, which I have called the posterior apodemes (pap). A transverse, fan-shaped and nearly semicircular apodeme arises from the posterodorsal surface of the vesica; this is the dorsal apodeme (dap). It has a thickened median keel at the base of which is an almost hemispherical, heel-like piston that compresses the vesica when muscles between the dorsal and lateral apodemes are contracted. Muscles between the dorsal and posterior apodemes serve to dilate the vesica. From the vesica, the penis curves forward and downward, within a membranous pouch, through the seventh segment to the floor of the eighth and so out through the adminiculum. The membranous pouch could be regarded as a narrow but deep continuation of the genital chamber, as it is open to the outside at the adminiculum.* The membrane is suspended at either side from the adminicular rods, the anterior end of the pouch being closed

* In some species of *Tipula* I have examined, the opening continues cephalad between what appear to be equivalents of the adminicular rods.

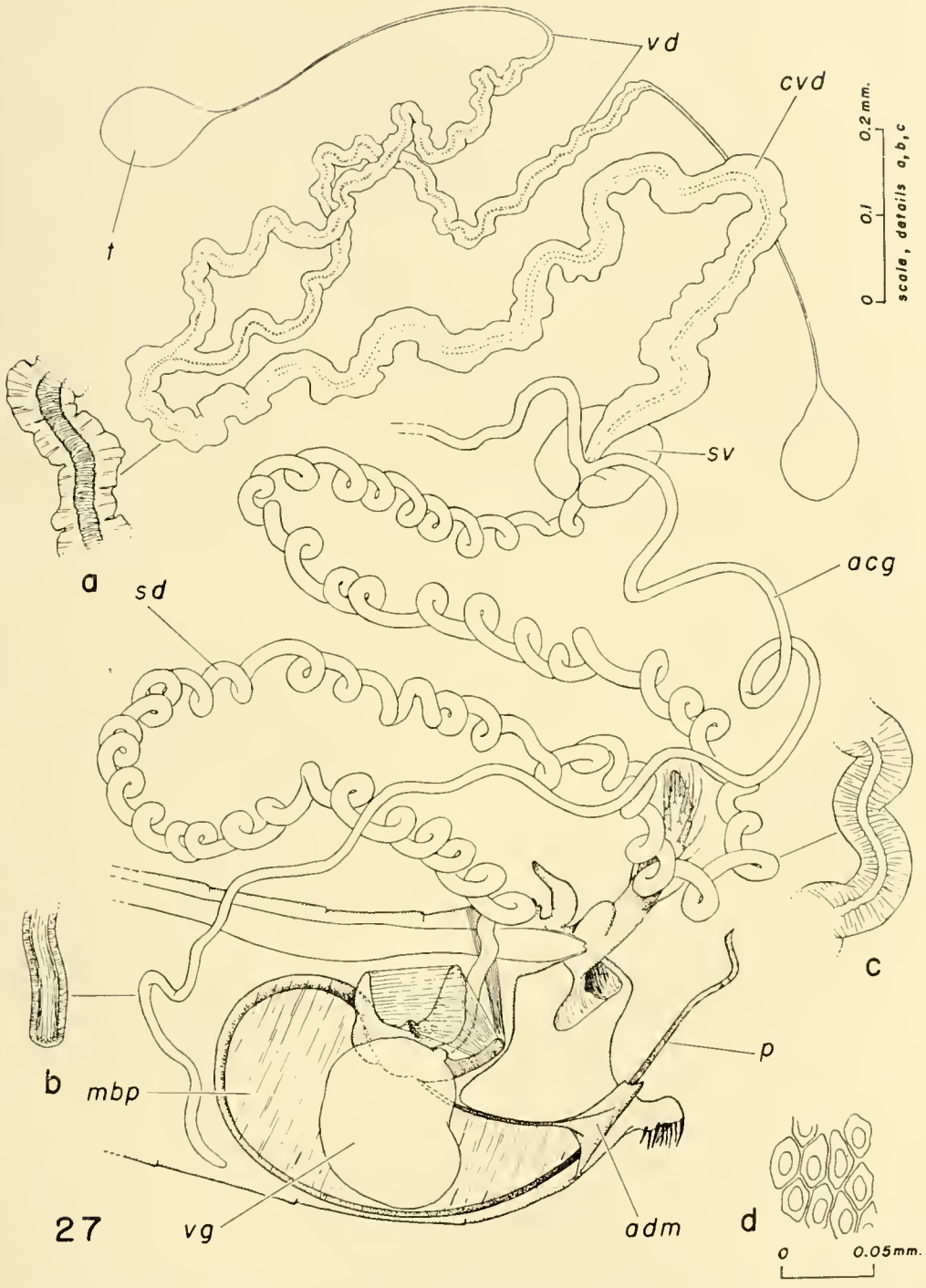


FIG. 27. Details of reproductive system of male *Dolichopeza (Oropeza) polita* ssp.; acg—accessory gland, adm—adminiculum, cvd—common vas deferens, mbp—membranous pouch enclosing penis, p—penis, sd—seminal duct, sv—seminal vesicle, t—testis, vd—vasa deferentia, vg—vesicular gland. Enlarged insets: a—common vas deferens, b—accessory gland, c—seminal duct, d—vesicular gland.

beneath the vesica and around the base of the penis. Contraction of muscles originating on the ninth sternum and inserting on the anterior faces of the lateral apodemes brings about rotation of the vesica and exsertion of the penis, which action is aided by small muscles connecting the posterior apodemes with the ninth tergum.

The nonsclerotized parts of the male reproductive system are usually complexly intertwined and difficult to disentangle. They have rarely been examined in detail in any Tipulidae (see Keuchenius, 1913) and, so far as I am aware, never in the genus *Dolichopeza*. I have unraveled this mass of tubes in most species of North American *Dolichopeza* and have found a rather consistent pattern, illustrated by the example of *Dolichopeza* (*Oropeza*) *polita* ssp., in Figure 27. There are two thin walled, bladder-like testes (t), which usually lie one before the other near the anterior end of the mass of the reproductive system. In a freshly-killed fly, these are usually found full of spermatozoa. The testes empty into the vasa deferentia (vd), which are at first exceedingly slender, then thick-walled and finally merged into a common vas deferens (cvd) with thick, irregular, possibly glandular walls enclosing a more or less central tube (Fig. 27a). The vasa deferentia are hyaline in appearance and are easily recognized among the abdominal contents by their glossy sheen.

The common vas deferens terminates in the center of an enlarged, ring-shaped, glandular-walled seminal vesicle (sv). That this structure, and not the enlarged parts of the vasa deferentia (cf. Snodgrass, 1935: 568), is actually the seminal vesicle is indicated by its comparatively large lumen, in which masses of spermatozoa have been observed. Two elongate "accessory glands" (acg) also converge and join at the seminal vesicle. These tubular glands are of a diameter about equal to that of the Malpighian tubules, with a relatively large lumen and walls of apparently columnar cells (Fig. 27b). Their color in life is pale rusty, with a granular appearance, but preserved in alcohol they are a dull white. The connection of the seminal vesicle to the other organs is not easily traced; however, it appears that it joins them at one end only, the other end being looped around the bases of the vas deferens and the accessory glands until it touches the end with the opening.

From the confluence of all these organs, a long and much-coiled conduit leads to the posterior side of the vesica, between the posterior apodemes. This has been called the ejaculatory duct (Keuchenius, 1913, for *Tipula* sp.), but because I believe that term hardly describes its function, I have called it simply the seminal

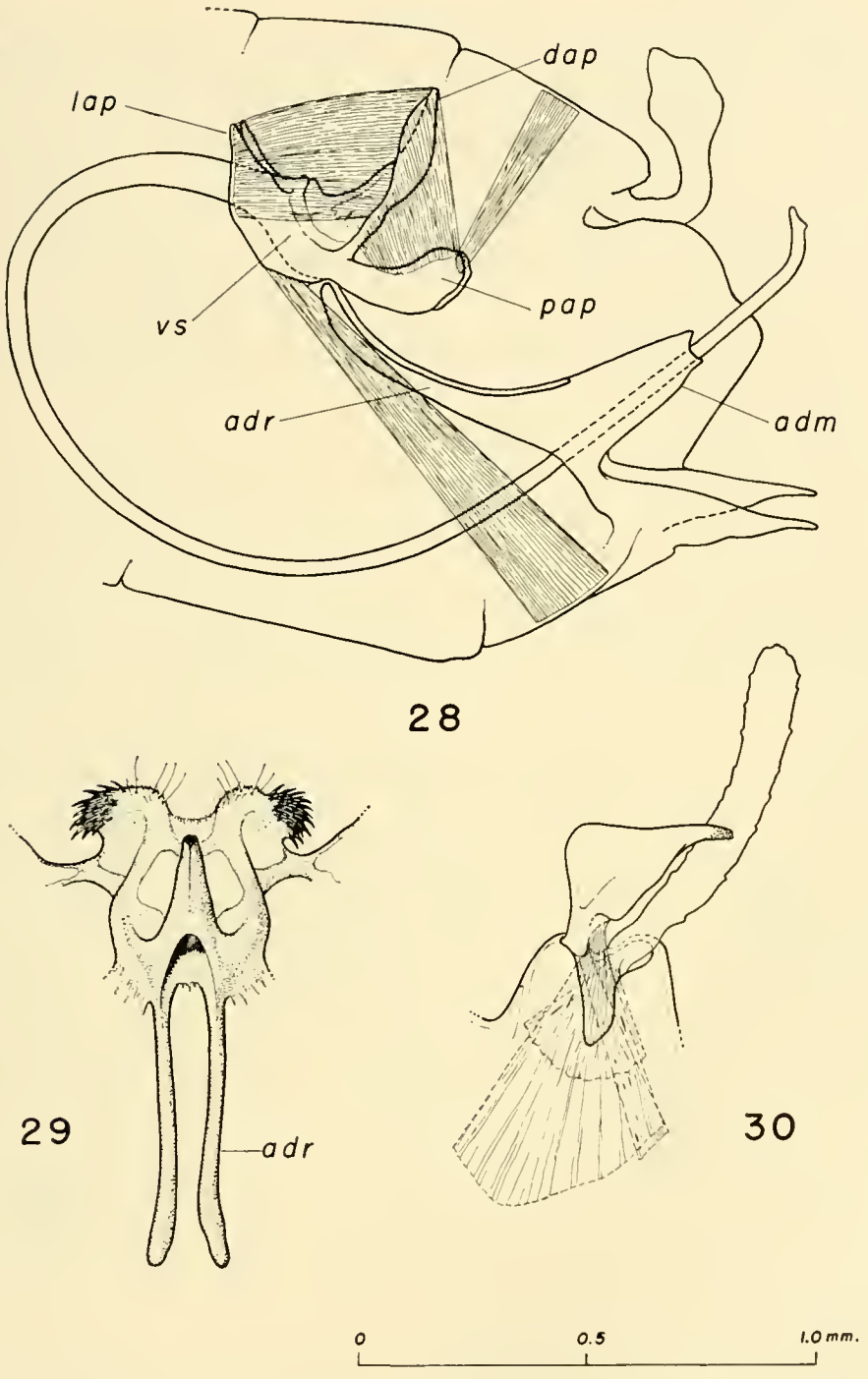


FIG. 28. Reproductive structures of male *Dolichopeza (Oropeza venosa;* adm—adminiculum, adr—adminicular rods, dap—dorsal apodeme, (compressor apodeme) of vesica, lap—lateral apodeme, pap—posterior apodeme, vs—vesica. FIG. 29. Reproductive structures of male *Dolichopeza (Oropeza) polita* ssp., dorsal aspect, showing relationship of adminiculum, adminicular rods and gonapophyses; adr—adminicular rod. FIG. 30. Left basistyle and dististyles of male *Dolichopeza (Oropeza) walleyi*, inner or mesial aspect, showing musculature (cf. Fig. 17).

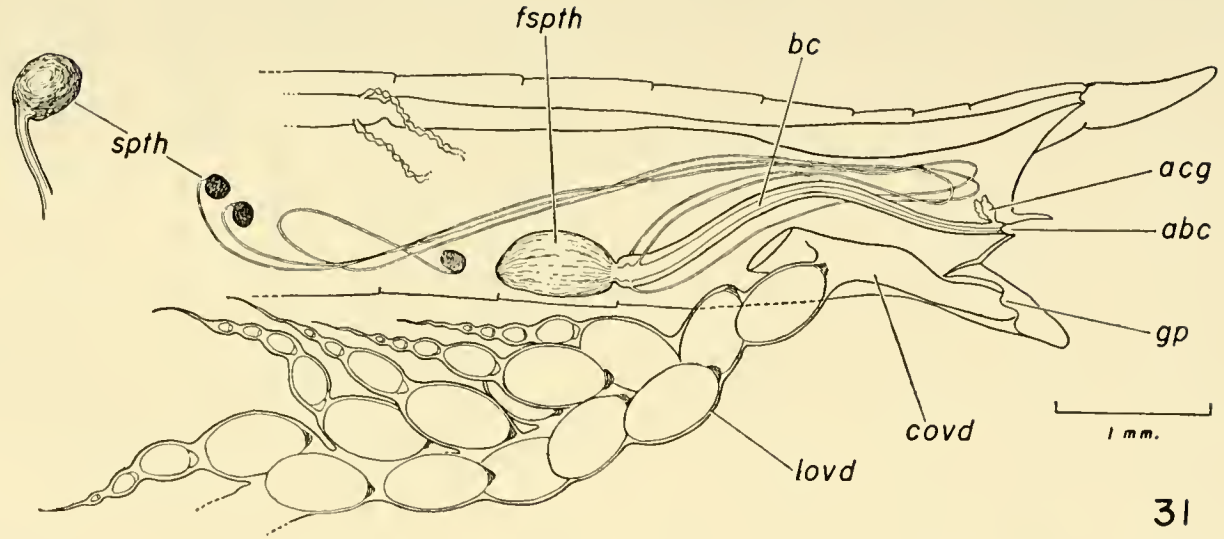
duct (sd). In species of the *obscura* group, the seminal duct is quite lengthy and is coiled in the manner of a spring, although the direction of coil is sometimes here and there reversed. Laid out more or less straight but with the small coils still in place, the seminal duct in a male *Dolichopeza* (*O.*) *polita* ssp. measured 23 mm. In *D. americana* and the *sayi* group, this duct is shorter and less tightly coiled, as a rule. In *D.* (*O.*) *carolus,* it is only about one-fourth to one-third as long as in *polita* but equally coiled and of about the same diameter as in the latter species. In *carolus* also the basal parts of the accessory glands are widened, rather resembling the common vas deferens.

Over-all length of the reproductive system from the vesica to the testis is about 45 mm., in larger species of the *obscura* group. From the seminal vesicle to the testis was 21.2 mm. in *obscura;* the common vas deferens measured 11.5 mm. in *polita.* In *americana* and the *sayi* group, the total length is about half as great, the difference in length of the seminal duct accounting for most of the decrease.

Perhaps most conspicuous among the nonsclerotized male reproductive organs are a pair of large, flattened, broadly reniform glands lying one at each side and somewhat below the vesica. Earlier authors seem not to have noticed these, but I have seen similar glands in *Tipula* spp. and other crane flies. They seem to reach their greatest development in *Dolichopeza.* The outer walls of these are smooth, but the inner surfaces have a vertically corded appearance and are made up of large, irregularly polygonal cells with large nuclei (Fig. 27d). The glands possess a lumen of capacity at least equalling that of the seminal vesicle and empty by ducts on their upper medial surfaces directly into the vesica. Judging from their size, they must contribute very significantly to the seminal fluid. The designation vesicular glands (vg) seems appropriate for these.

Female reproductive system.—The reproductive apparatus of the female *Dolichopeza* is divided into two portions: the bursa copulatrix and its associated structures, and the oviducts and their ovarioles. These two parts have separate external apertures, as discussed earlier under the external morphology of the females, and they seem to have no internal connections.

Leading cephalad from the gonopore is a thin-walled but muscular common oviduct (Fig. 31, covd), which in about the middle of the seventh abdominal segment divides into two lateral oviducts (lovd). These organs, because of their membranous structure, are



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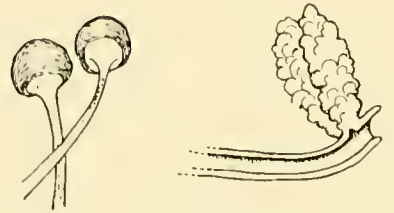

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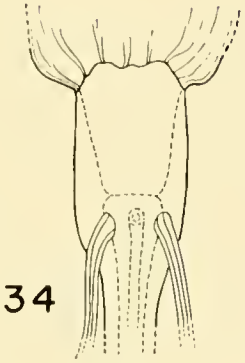

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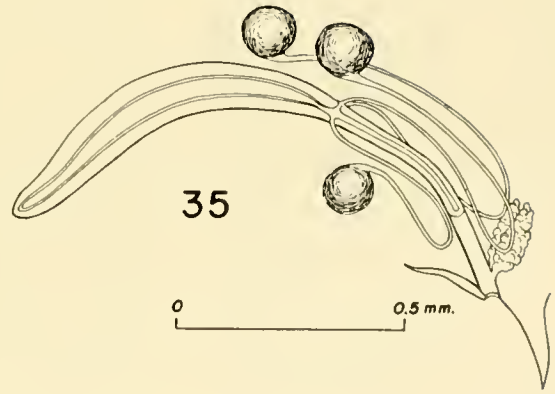

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FIG. 31. Internal reproductive structures of female *Dolichopeza (Oropeza) tridenticulata;* abc—aperture of bursa copulatrix, acg—accessory glands, bc—bursa copulatrix, covd—common oviduct, fspth—functional spermatheca, gp—gonopore, lovd—lateral oviduct, spth—spermatheca. FIG. 32. Two spermatheeae of *Dolichopeza (Oropeza) carolus.* FIG. 33. Same as 31; detail of accessory glands. FIG. 34. Same as 31; anterior end of bursa copulatrix, dorsal aspect, showing attachment of spermathecal ducts. FIG. 35. Internal reproductive structures of female *Dolichopeza (Dolichopeza) americana.*

most easily seen in older females that have laid practically all their eggs. From each lateral oviduct, lying along the floor of the abdomen, the many ovarioles rise dorsally and bend anteriorly, their filiform tips often attaching to the dorsal or lateral abdominal walls. Within the ovarioles, eggs in increasing stages of development may be seen, from scarcely discernible specks in the upper ends to well formed but still pale colored eggs toward the lateral oviducts. In a newly-emerged female, the lateral oviducts and lowermost portions of the ovarioles are stretched taut with fully formed eggs, in which the chorion is already black and the terminal filaments (in those species that have them) completely developed. The eggs lie with their posterior ends directed toward the gonopore, which is also the way they are oriented in the ovarioles. In gravid females, eggs are found as far forward as the first abdominal segment, compressing the viscera tightly against the body wall.

In copulation, the penis of the male is inserted into the bursa copulatrix (bc), and the spermatozoa are presumably stored in the three spermathecae until the time of oviposition. The spermathecae (spth) are very small, intensely sclerotized capsules that are the only structures besides eggs to show at all clearly in flies that have been treated with KOH for mounting on microscope slides. They connect to the anterior end of the bursa copulatrix by filamentous ducts, two of which join the bursa dorsolaterally and one ventrally (Fig. 34). Their shape is nearly spherical in most species but flattened on the side of attachment in *Dolichopeza carolus* (Fig. 32). The spermathecal ducts are of great length and are thrown into long loops within the abdomen. In teneral females, the distal ends of these ducts, that is, the ends nearest the spermathecae, are soft, wrinkled and coiled. In older females, however, the ducts grow firmer, straighten out, and elongate, as the spermathecae move from the anterior end of the abdomen toward the middle or posterior regions. In *Dolichopeza americana*, the spermathecal ducts are shorter, and the spermathecae are usually found near the caudal end of the abdomen in both teneral and older flies (Fig. 35).

In species of the subgenus *Oropeza*, the bursa copulatrix extends cephalad to the sixth or fifth abdominal segment, while in *Dolichopeza* s. s. it is much shorter, scarcely half a millimeter in length (compare Figs. 31 and 35). The bursa has a thin, yellowish lining and a thick, whitish-transparent outer wall. A pair of nodular, whitish accessory glands (acg), the function of which in

these flies is unknown, open into the bursa copulatrix on its dorsal wall near the aperture (Fig. 33).

A relatively large pouch joins the anterior end of the bursa copulatrix, only a short distance from the attachment of the spermathecal ducts. It is rather oval in shape, with thin wrinkled walls in species of the *obscura* group (Fig. 31), thicker-walled and more elongate in the *sayi* group, and rigidly thick-walled, elongate and curved in *Dolichopeza americana* (Fig. 35). Its connection to the bursa is somewhat different from species to species in *Oropeza*, as will be seen on comparison of Figures 31 and 34. Unable to find any structure in any other insect that is homologous with this pouch, and noting the wide opening from the pouch into the bursa copulatrix, I am inclined to regard the pouch as the functional spermatheca (fspth) and to suspect that the three small spermathecae are generally nonfunctional in *Dolichopeza,* and perhaps in other Tipulinae. This supposition finds some support in the fact that oviposition takes place very soon after mating and that the eggs are fertilized at the time of deposition, presumably by a flow of seminal fluid over them sufficient to insure that some spermatozoa will reach the micropyle of each egg; hence the supply of spermatozoa is presumably large and situated rather near to the opening of the oviduct. The spermathecae, on the other hand, are quite small, and their ducts are in some species nearly twice the length of the entire abdomen. It may be, of course, that the large pouch stores sperm for rather immediate use, while the spermathecae are reservoirs for several hours' on days' storage.

INTRASPECIFIC VARIATION

After studying many individuals of a species, it is possible to conclude, somewhat reliably, what is the normal or usual condition of practically any observable feature of the organism involved. On this basis, it is possible also to visualize an average individual of the species, in which means of dimension, color, shape and so on are combined. Then, all specimens at hand will be seen to deviate, in one way or another and to varying degrees, from the average. Small departures of common occurrence may, I believe, be regarded as falling within a normal range, while extraordinary individuals may be considered abnormal. It is also found, from time to time, that with respect to one or more characteristics individuals may group around two or more distinct means, in which cases special interpretation is required, for clines or geographic races may be indicated.

Some of the individual, intraspecific variation in *Dolichopeza* has

been misinterpreted, as it has also in many other groups of organisms. It therefore has seemed worthwhile to attempt to classify the kinds of variation encountered and to indicate their probable causes. The classification that follows is not intended to be general in scope but applies only to variation observed in *Dolichopeza*. The kinds of variation include:

1. Seasonal, or ecological, size variation.
2. Color variation.
3. Morphological variation, both
   A. Growth anomalies (all of which are abnormalities) and
   B. Inherited differences, which may constitute
      (1) abnormal morphological variation, or
      (2) normal morphological variation.

Size variation.—Over-all size of individual flies appears to be affected markedly by conditions in the larval habitat. Larvae of *Dolichopeza* inhabit mosses and liverworts, which ordinarily grow most luxuriantly in the spring. Adult flies emerge at two times each year, in most species and in most parts of the range of the genus, there being flight periods in the spring and again in the late summer or early fall. Those larvae which give rise to the spring generation of adults feed in the autumn, become quiescent in winter and feed further in early spring, while those developing into adults of the fall generation, being progeny of the spring adults, feed only during a period of about two and a half to three months in the summer, when their moss habitat is usually drier than at other times of the year. That the fall generation adults in all species are of smaller size than those of the spring generation appears to reflect this variation in larval habitat. This is further suggested by the fact that spring generation adults reared in the laboratory, where they are subjected to various inadequacies of environment, are smaller than flies of that generation occurring in nature. Of course, there is size variation among flies of a single generation, which may result from fluctuations in larval environment or may be due to other, less understood causes.

Seasonal variation is well illustrated by *Dolichopeza americana*. On the assumption that wing length is a reliable index of over-all size of the fly, wings of ten males and ten females representing each generation were measured and compared (Table 1). All spring generation flies were captured between 10 and 25 June and those of the autumn generation all on 4 August; and all specimens were collected within the same general habitat, within a radius of 200 yards, at a locality in west central Indiana. The flies were taken

TABLE 1.—Wing Length in *Dolichopeza americana* (Measurements in Millimeters)

	Generation	Mean	Range	Median
Males	Spring	10.3	9.2-11.1	10.4
	Fall	8.4	7.2- 9.1	8.7
Females	Spring	11.4	11.0-12.9	11.2
	Fall	9.4	8.9-10.1	9.2

at random from specimens stored in opaque paper envelopes. In this instance, the means in both males and females are widely separated, and it may be seen from the table that the ranges of wing length of spring and fall flies do not even overlap. This is a rather extreme example, but it illustrates the tendency seen in the other species.

Color variation.—Color of preserved specimens is greatly affected by their age, exposure to sunlight, and method of preservation. In specimens only a year or two old, as well as in living material, there is sufficient variation in coloration to indicate that ordinarily no reliance can be placed on slight differences of shade or color for taxonomic purposes. Where I have referred to color in describing species, especially in the key to adult females, I have tried to limit its use to color patterns or to general coloration, used in conjunction with other characters. It is very difficult to communicate one's estimate of color to another person, and because the colors in *Dolichopeza* are not fixed enough to be referred to a standard color guide, it has seemed best to omit discussion of color details.

There are, however, a few examples of significant intra-specific variation in color in North American *Dolichopeza,* the most outstanding of which is that found in *D. walleyi.* This species in general appearance rather closely resembles another, namely *D. sayi.* In northeastern United States and southeastern Canada, where the ranges of the two species broadly overlap, they are distinctly colored. *D. sayi* has darkly spotted thoracic pleura, nearly black stripes on the prescutum, and darkly sclerotized hypovalves in the ovipositor of the female; in contrast, *D. walleyi* has pale thoracic pleura, reddish brown prescutal stripes, and paler hypovalves in the female. Specimens of *D. walleyi* from localities a short distance outside the range of *D. sayi* have coloration suggestive of some sort of mixture of those described, and populations of *walleyi* from Florida, Iowa and South Dakota (that is, from localities furthest from the range of *D. sayi*) are very like *sayi* in the intensity of their markings. This phenomenon has been described as character displacement (Brown and Wilson, 1956).

Growth anomalies.—I have occasionally discovered an individual having a very unusual deformity, which by its rarity and nature appears to be the result of defective development rather than the effect of an unusual gene or combination of genes. In *Dolichopeza tridenticulata,* for example, the posterior margin of the ninth tergum of the male abdomen bears a three-pointed projection such as that shown in Figure 59; but the presence of a foreign particle in the tissue of the tergum resulted in the deformity illustrated in Figure 36. Another growth anomaly is the extraordinary enlargement and sclerotization of the apex of one of the inner dististyles of *Dolichopeza polita,* compared with the normal structure of the opposite appendage in the same individual (Fig. 37). Growth abnormalities may affect any stage in the life history. For example, a pupa of *D. obscura* lacked one lateral lobe of the series of four ordinarily occurring in a transverse row on the eighth sternum (Fig. 38). Above the spiracular region of the larva of *Dolichopeza,* there are four subconical, fleshy lobes, the middle two of which are shorter than the others and situated close together, one at either side of the midline. However, among many hundreds of larvae of all species examined, there was found one specimen in which these two median dorsal lobes had grown together (Fig. 39). This individual, incidentally, showed the normal structure in the next earlier instar. All anomalies of the sort here described have been seen only once among the many thousands of flies examined.

Inherited differences.—Other morphological differences seem to have their basis in the genetic makeup of the insects. Among these are several abnormalities that recur with varying frequencies, either throughout the range of a particular species or scattered throughout the genus. The habitats of *Dolichopeza* are discontinuous in most of the range of the genus in North America, and as a result of this there is probably a great deal of local inbreeding. This, at least, would account for the fact that certain abnormalities are locally quite common. Perhaps the most readily observed of such characters is wing venation, the usual pattern of which in subgenus *Oropeza* is presented, in part, in Figure 40. Now, throughout most of its wide range, *Dolichopeza tridenticulata* has the normal wing venation of this subgenus, but in central and southern Indiana, local populations of this species may have as high as 40 to 55 percent incidence of deformity of the medial field, that is, of the branches of the media. Figures 41 through 47 illustrate wings of *D. tridenticulata* in which deformity of the discal cell, a shift of

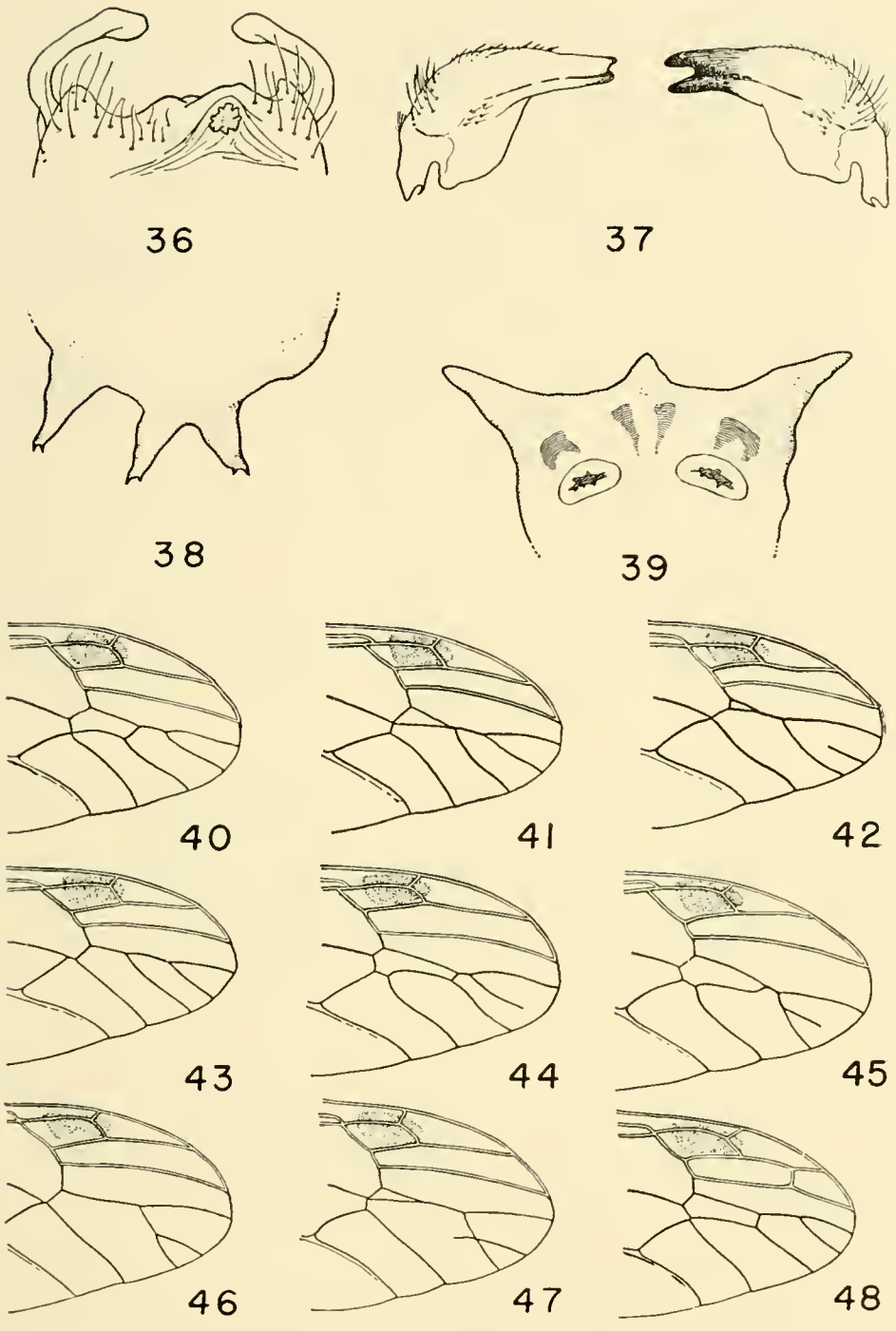


FIG. 36. Abnormal development of ninth tergum of male *Dolichopeza (Oropeza) tridenticulata* due to presence of foreign body. FIG. 37. Inner dististyles of male *Dolichopeza (Oropeza) polita* ssp., showing abnormal development of apex of left dististyle. FIG. 38. Eighth sternum of pupa of *Dolichopeza (Oropeza) obscura,* showing abnormal development of spinous processes. FIG. 39. Spiracular disc of larva of *Dolichopeza (Oropeza) sayi,* showing abnormal (fused) dorsal lobes. FIGS. 40-48. Variations in wing venation in *Dolichopeza (Oropeza) tridenticulata;* 40—normal venation, 41-47—aberrations of the medial field in a population from central Indiana, 48—spurious cross-vein in cell R_3 in a population from southern Minnesota.

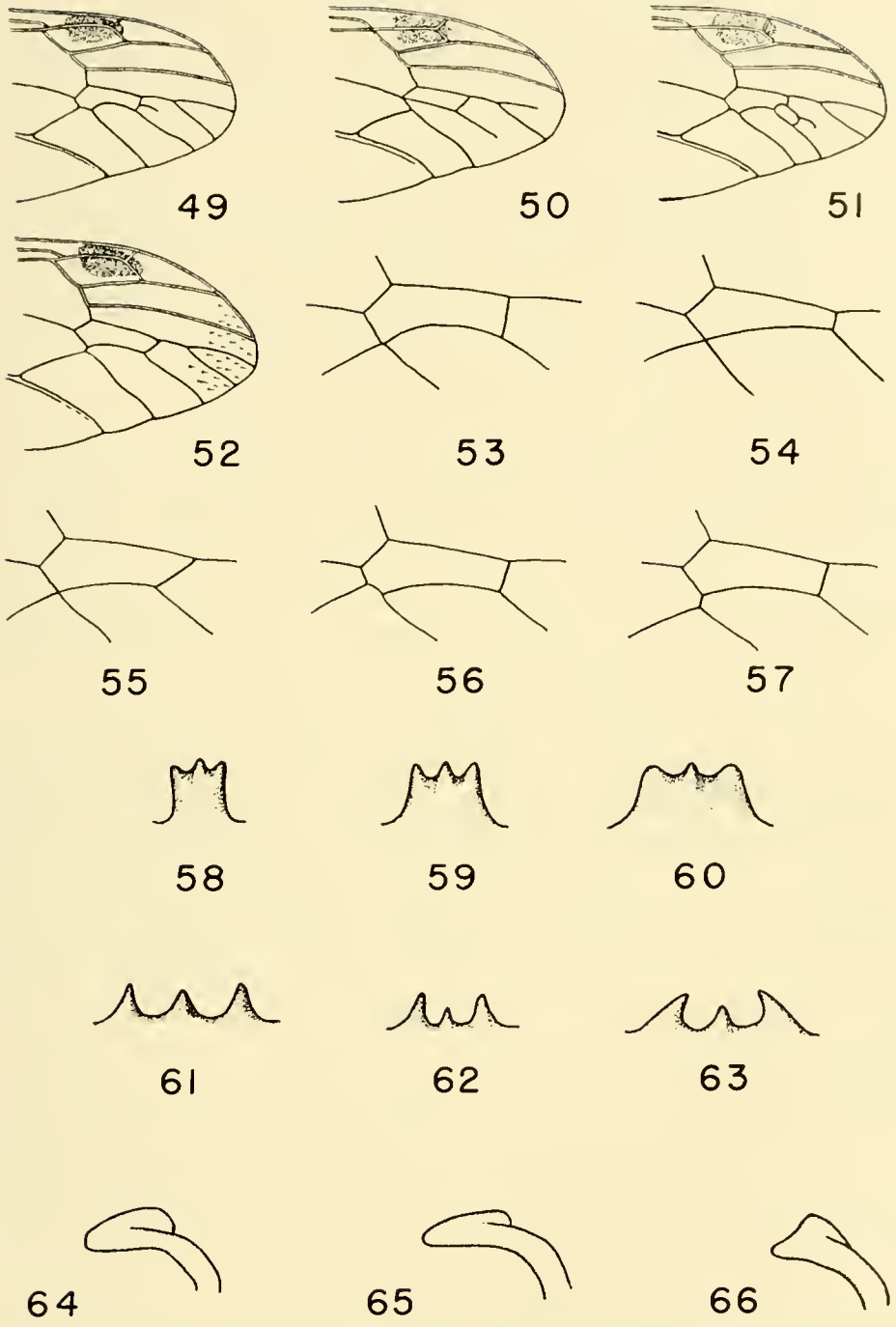
the base of the vein M_2 from M_1 to M_3, and other abnormalities may be seen. Figure 43 is particularly interesting in that the discal cell is completely absent, and the m-cu cross-vein has shifted so as to join the media before its first branching, a combination of characters typical of the venation of the subgenus *Dolichopeza*! Among specimens of *D. subalbipes* from the southern part of the range of the species, there are many similar deformities of the medial field. Some of these, one even resulting in an extra closed cell beyond the discal cell, are shown in Figures 49 through 51.

A further, rather remarkable example of this kind of intraspecific variation is shown in Figure 48. A spurious cross-vein in cell R_3 of the wing is extremely uncommon anywhere in the genus; yet, in one locality in Minnesota, ten *Dolichopeza tridenticulata* in a sample of thirty specimens had such a cross-vein in one or both wings. The venation of these flies was in other respects normal. Venational aberrations of sorts similar to those described here have been observed in the mosquito, *Culex pipiens*, in which species they have been found to be controlled by single mutant genes (Laven, 1957: 452 ff.).

The occurrence of macrotrichia in the apical cells of the wing is similarly uncommon throughout the North American species of *Dolichopeza*, but in *D. walleyi* this variation has appeared in a few populations in scattered parts of the range (Fig. 52).

In contrast to such striking departures from the usual condition, there are several morphological variations of lesser degree that are so often found in almost any population of a species that I think they may be considered as normal variation, just as we recognize certain differences in detail of facial features among normally appearing human beings. These slight modifications of form are probably genetically controlled, although no study of this has been made. Examples are found in all species of *Dolichopeza*, and within each species such characteristics seem to be distributed at random, or nearly so. That is to say, in any population throughout the species' range, all known variations of the particular character may occur. Such differences include minor shifts in the positions of various wing veins with respect to the discal cell (Figs. 53 through 57) and slight modifications of the caudal margin of the ninth tergum or the tergal arms in males (Figs. 58 through 66). Many other examples could be cited, but these will serve to illustrate the point.

Dolichopeza tridenticulata takes its name from the three-toothed projection on the ninth tergum of the male, a structure ordinarily



FIGS. 49-51. Aberrations of the medial field in wings of *Dolichopeza (Oropeza) subalbipes;* 49—specimen from Florida, 50—Georgia, 51—Alabama. FIG. 52. Wing of *Dolichopeza (Oropeza) walleyi* from Michigan, showing macrotrichia in apical cells. FIGS. 53-57. Variations in shape of discal cell (cell 1st M_2 occurring commonly in *Dolichopeza (Oropeza)* spp. FIGS. 58-60. Normal variation in medio-posterior margin of ninth tergum of male *Dolichopeza (Oropeza) tridenticulata.* FIGS. 61-63. Normal variation in medio-posterior margin of ninth tergum of male *Dolichopeza (Oropeza) obscura.* FIGS. 64-66. Normal variation in lateral arms of ninth tergum of male *Dolichopeza (Oropeza) walleyi.*

having a shape like that shown in Figure 59. However, in any sample of several males of this species, one may expect to find the projection more slender, as in Figure 58, or broader and with the points more rounded, as in Figure 60. Likewise, in *D. obscura,* the median posterior teeth of the ninth tergum, most often having the form of Figure 62, may be variously spaced and deflected, as indicated in Figures 61 and 63. Shapes of the apices of the tergal arms in *D. walleyi* may vary as indicated in Figures 64 through 66, not only from one individual to the next but from side to side in the same fly.

In all species of the subgenus *Oropeza,* slight variations in the positions of veins about the discal cell are commonly seen. For example, the m-cu cross-vein may join M_{3+4} (Fig. 56) or M_4 alone (Fig. 57) instead of intersecting the junction of these veins as in Figure 55. A common venational variation in all species of *Oropeza* is the presence of the short segment of the vein M_4 between the discal cell (cell 1st M_2) and the junction with the m-cu cross-vein (Fig. 57). This short length of M_4 has been called the m-cu cross-vein in the nomenclature of Comstock and Needham (see Needham, 1908), who regard the vein M_4 as an anterior branch of the cubitus. Following this system, Johnson often refers, in his descriptions of new species of *Oropeza,* to the presence or absence of the short m-cu cross-vein. Within the *obscura* group, the cross-vein m may cross rather perpendicularly or diagonally from M_{1+2} to M_3 (compare Figs. 53 and 55), and it may be quite short (Fig. 54).

Since these characters may be expected in any sample of several individuals from any locality within the range of a species, and since they appear to have no correlation with geographic distribution and fall easily within the limits of variation of the species, they must be considered as having no taxonomic significance.

In the case of coloration in *Dolichopeza walleyi* already mentioned, the change from one kind to the other is clinal in nature. Not only would it be difficult to distinguish clearly two geographic races, in this instance, but naming them would serve no useful purpose. Variation may not be such a continuous gradation between extremes, however, but rather a regional preponderance of a particular phenotype, or phase. In *Dolichopeza subalbipes,* for example, the lateral arms of the ninth tergum of males are of two types, one with a very slightly expanded tip (as figured by Alexander, 1942: 213) and the other with a greatly enlarged, or inflated, bulbous tip. In the southern United States, the latter form is domi-

nant in all populations, while the narrow tipped form is almost a rarity. In the northernmost states and in Canada, however, the slender tergal arm is much more common. In any one population, both types are likely to occur, so that this cannot constitute either a cline or a subspecific difference. I have seen only a few specimens that seem to be intergrades between the two extremes. On the other hand, if it is possible to demonstrate that the grouping of individuals of a species around two or more means is somehow correlated with geographic distribution, then subspecies may be indicated. In *Dolichopeza polita*, for example, characteristics of coloration, male genitalial structures, and other features of adult and immature forms are generally grouped around three different means, allopatric in distribution but with zones of intergradation at the borders where they meet. These seem to fulfill the requirements of subspecies, as will be discussed later in detail, and it has been found useful in this case to apply names to the three groups.

ADULTS—NATURAL HISTORY

Longevity.—The adult life of *Dolichopeza* is quite brief. Rogers (1933: 29) estimated a maximum duration of adult life of tipulines to be three weeks, but I would judge the maximum for *Dolichopeza* to be little more than half that. Flies kept in the laboratory without food lived from two to four days following emergence, while those that were provided with sugar-water remained alive in some instances as long as six days. The cooler temperatures of natural environments would probably decrease the metabolic rate, allowing the flies to live somewhat longer, and it seems likely that natural sources of nourishment for both the larva and the resulting adult would be a factor in longevity.

Distribution.—Practically the only activities of adult *Dolichopeza* are those related to reproduction. These are discussed in detail in the sections on mating behavior and oviposition which follow. But the geographical, ecological and seasonal distribution of species of *Dolichopeza* present certain problems possibly bearing on reproductive activities. It seems not unreasonable to expect that if species are very closely related there might be occasional flow of genes between them, unless they are somehow wholly isolated from each other. Most species of North American *Dolichopeza* fall together with one or more other species into groups with very close interrelationship, the species in some instances so nearly identical as to be distinguishable only by microscopic examination. This being the case, it becomes important to know if there is cross-

mating between any two recognized species, either regularly, occasionally, or at all. If there is any exchange of genetic material of one kind of *Dolichopeza* with any of its relatives, it must of course take place in the adult stage. Consequently, it is worthwhile to know what opportunities these flies have for cross-mating; that is, where do the adults of the different forms meet and intermingle geographically, ecologically and seasonally?

That there is some ecological separation of the species has already been indicated (p. 672). Darkly-colored species are usually taken in deeply-shaded situations, and those having various patterns of dark on buffy yellow are usually found in the more open shade of forest and marsh vegetation. The general environment itself can be divided into three categories, insofar as *Dolichopeza* is concerned; these are rocky gorges and ravines, forests, and marshes, bogs and swamps. Even where these broad types of habitats meet, as where rocky gorges occur in forests, the species of *Dolichopeza* demonstrate a marked degree of ecological separation.

It is, of course, the microhabitat that determines the presence or absence of a species. It is nevertheless possible to divide the North American species into three groups, based upon the three major kinds of habitats named, for within these habitats occur the microenvironments that meet the particular needs of the species. Characteristic of rocky gorges and ravines of the Appalachian Mountains are *Dolichopeza americana, carolus, johnsonella, obscura, polita, tridenticulata, walleyi,* and, depending on the part of the mountains, *subvenosa* or *venosa.* Of these, *carolus* and *walleyi* are more specifically associated with leafy vegetation along the sides of the ravines, while *subvenosa* or *venosa* are found either in such vegetation or together with the other species in nearly any deeply-shaded crevice or cranny. The same association of species is found west of the Appalachians in places where irregularities in the terrain afford conditions similar to those of mountainside ravines, except that *subvenosa* is replaced by *venosa.*

In cool, mesic forests, the favorite haunts of *Dolichopeza obscura, walleyi* and sometimes *tridenticulata* and (within its range) *subvenosa* are hollows in standing or fallen trees, cavities beneath outcropping rocks, undercut banks, or about the roots of windthrown trees, but *walleyi* may occur also out among the lower plants, where *subvenosa, venosa* and *carolus* are sometimes found.

Those species encountered most often in bogs, swamps and marsh borders include *Dolichopeza dorsalis, sayi, similis* and *subalbipes,* although such habitats are commonly occupied also by

obscura (again seeking out the deepest shade) and sometimes by *americana.*

Data on seasonal distribution of adults are based mostly upon dates of capture. I have not often worked in one locality long enough to learn precisely the order of appearance of each species and how long it was present as adults. Observations made in 1953 at a particular cavity in a rock cliff in Turkey Run State Park, Parke County, Indiana, showed *Dolichopeza americana* to be the earliest species, appearing on 18 May and reaching a spring peak of population about 26 May. *Dolichopeza polita* ssp. first appeared on 23 May and reached a relatively high peak, exceeding the numbers of all other species together, on the 29th and 30th of May. On the 28th of May, *D. walleyi* and *obscura* were found with the others, but in much smaller numbers. Four days later, *tridenticulata* appeared, making five species represented in the sample of 142 flies taken on 1 June from that one rather small cavity, which had perhaps ten or twelve square feet of roof surface from which the flies were suspended. All these were taken with a single sweep of the net, and at other times it was possible to take a sixth species in the same place, together with the five named.

It will possibly occur to the reader that this is an unusual situation and that localities in which several species of *Dolichopeza* exist side by side as adults are really uncommon. But the fact is that what I have described for the Indiana locality can be duplicated in many parts of the North American range of the genus. (And in Korea, in a rather similar environment, I found four species of *Dolichopeza* together in crannies of a cliff in early June.) The following data from my own collections will bear out this statement:

Ohio, Portage County, Nelson Ledges State Park, 24-25 June 1953: *americana, carolus, johnsonella, polita* ssp., *subalbipes, tridenticulata, venosa* and *walleyi.* On another trip to this place I took also *obscura.* Total: 9 species.

Virginia, Rockingham County, Dry River, 6 July 1952: *americana, carolus, obscura, tridenticulata* and *walleyi.* Total: 5 species, in a sample of 12 specimens taken in about ten minutes of collecting just before a rainstorm.

North Carolina, Burke County, Linville Falls, 14 June 1958: *americana, carolus, obscura, polita* ssp., *subvenosa, tridenticulata* and *walleyi.* Total: 7 species among 27 specimens collected.

Georgia, Union County, Neel's Gap, 10 June 1958: *americana, carolus, johnsonella, obscura, subalbipes, subvenosa* and *tridentic-*

ulata. In a collection made at this place on 28 June 1952, I took also *polita* ssp. and *walleyi.* Total: 9 species.

Virginia, Giles County, near Mountain Lake Biological Station, 21 June 1958: *americana, carolus, obscura, subalbipes, subvenosa, tridenticulata* and *walleyi.* Other collections at this locality yielded also *johnsonella* and *polita* ssp. Total: 9 species.

Maine, Cumberland County, near Bridgton, 1 July 1953: *americana, obscura, sayi, subalbipes* and *walleyi.* Total: 5 species among 7 flies of the genus found.

West Virginia, Pocahontas County, Droop Mountain Battlefield State Park, 23 June 1958: *americana, johnsonella, obscura, tridenticulata* and *walleyi* all together among the rafters of one picnic shelter. In the same state and county, a few miles away in Watoga State Park, 5 July 1952: *americana, carolus, obscura, polita* ssp., *subalbipes* and *tridenticulata.*

Pennsylvania, Luzerne County, Ricketts Glen, 10 July 1952: *americana, carolus, johnsonella, obscura, polita* ssp. and *tridenticulata.* In four different collections, here, in three different years, I have never found *walleyi,* but I am confident it will be added to the list.

Ohio, Hocking County, "Neotoma" (a small valley near Rockbridge belonging to Dr. Edward S. Thomas of the Ohio State Museum), 30 May 1952: *americana, carolus, obscura, polita* ssp. and *tridenticulata.* On other occasions, I have also taken within this limited area *dorsalis, johnsonella, subalbipes, venosa* and *walleyi,* making a total of 10 species.

Great Smoky Mountains National Park (collections in Sevier County, Tennessee, and Swain County, North Carolina), 30 June 1952: *americana, carolus, obscura, polita* ssp., *subalbipes, subvenosa* and *tridenticulata.* Also taken in the park are *dorsalis, johnsonella* and *walleyi.* Total: 10 species.

Michigan, Washtenaw County, Mud Lake Bog (near Whitmore Lake), various dates: *americana, dorsalis, obscura, sayi, similis, subalbipes* and *walleyi,* often four or five species in any one collection.

Michigan, Livingston County, Edwin S. George Reserve (a natural area belonging to the University of Michigan, near Pinckney), various dates: the same species list as for Mud Lake Bog, except that *venosa* is added. Total: 8 species.

Wisconsin, Juneau County, Rocky Arbor Park (near Wisconsin Dells), 6 July 1950: *carolus, obscura, polita* ssp., *subalbipes, tridenticulata* and *venosa.* Total: 6 species.

Kansas, Douglas County, 15 miles south of Lawrence, 30 August 1957: *obscura, polita* ssp. and *walleyi.* These three species are from a locality that is probably near the western limit for the genus, at this latitude.

A great many more collection records similar to those presented here, particularly from the Appalachian region, could be mentioned, but these suffice to illustrate the point that where one species of *Dolichopeza* occurs, one or more others are likely to be found with it.

With two exceptions (*similis* and *venosa*), all the species of *Dolichopeza* that occur in eastern North America appear to have two generations per year in that part of their range lying roughly between the latitudes of northern Florida and New England. In Florida and southernmost Georgia, there are records of some species for nearly all months of the year, suggesting that the life cycle is repeated as often as biologically possible, with perhaps a dormant period in January and February of some years. While there seems to be no particular peak of abundance of individuals of any species at any season, in the Florida region, most of the collection records indicate that early summer (June) is a time when the numbers of most of the species are increased. From Georgia northward, particularly at higher elevations, there occurs a marked two-generation cycle, annually. In general, the peaks of emergence of adults come in late May and early June and again in August, but early and late emergence of individuals give considerable slope to these peaks. Available collection records from the northern edges of the range of the genus are insufficient to give a clear picture, but they suggest that a single mid-summer generation is the usual thing. Further collecting is needed especially in Canada to verify this. *Dolichopeza similis* and *D. venosa* are northern species, found only in the northeastern states and Canada, with a flight period from late May to early August, nearly all the records being for June and the later records being for the more northern parts of the range. More specific data on dates and localities of collections of adults will be found listed in the sections on the species concerned.

Activities.—Certainly the most spectacular activity of adults of *Dolichopeza* is their peculiar dancing flight. This is most easily observed in species of the *obscura* group because, somewhat restricted to certain niches by their reaction to the intensity of outside light, they will leave their darkened shelters by day only when greatly alarmed. Dropping from its resting position, the fly moves

in a rather elliptical path, first downward and backward, then rising and forward, keeping the head oriented more or less toward the original point of suspension. This cycle is repeated with such rapidity that the fly seems almost to fade from view, although the dance is limited to about a three-inch ellipse. The dance of *Dolichopeza carolus* is more conspicuous, mostly, I suppose, because of the paler colors of that species, which contrast somewhat with its leafy habitat. When disturbed from a distance, *carolus* moves in a more vertical ellipse, often six inches in length; but if approached closely, it usually moves away rather directly and hurriedly. It is my impression that the other species that are found most commonly in vegetation also take readily to flight when disturbed. This is particularly true of *dorsalis* and *sayi,* and I have never observed the elliptical flight in either of these species. Among the species of the deeply shaded, rock gorge habitat, those of the subgenus *Oropeza* seem much more restless than *D. americana;* they are more easily alarmed to the point of dancing and are slower to settle back to rest, and in the same respects, males are more restless than females. Spontaneous dancing during twilight formation of swarms, possibly related to mating activities, has been noted in *Dolichopeza johnsonella.* The dance of this species in the open air was observed to be nearly straight up and down, along a fairly constant path of about twenty inches in length, and the flight was markedly slower than that of the diurnal dance beneath a rock ledge.

During the daylight hours, the primary occupation of adults of *Dolichopeza* is resting in such shaded and protected haunts as are available within the general habitat. In repose, the flies almost invariably hang from some overhead support, such as the bottom of an outcropping rock, an undercut bank, the roof of a darkened drain tile or culvert, stems or leaves of low plants, or the eaves of buildings situated among trees. It has been observed that the number of legs used in suspension varies. Alexander (1919: 929-930) states that a point of distinction between the subgenera is that "*Oropeza* hangs . . . with only the fore legs attached . . . *Dolichopeza,* on the contrary, has the four anterior legs on the support, the hind legs dangling. . . ." I think this was a slip of the pen, for while one may observe considerable variation in the resting postures of both subgenera, it is *Dolichopeza americana* that is nearly always seen suspended by the two front legs only, with the four other legs held out to the sides, perhaps dangling

a bit (Fig. 67). Species of *Oropeza*, on the other hand, usually hang by both the prothoracic and mesothoracic legs (Figs. 68-70). Variations involving three to six legs are not uncommon in both subgenera. In fact, among more than a hundred *Dolichopeza* (*O.*) *polita* ssp. observed in an Indiana locality on two days in late May,

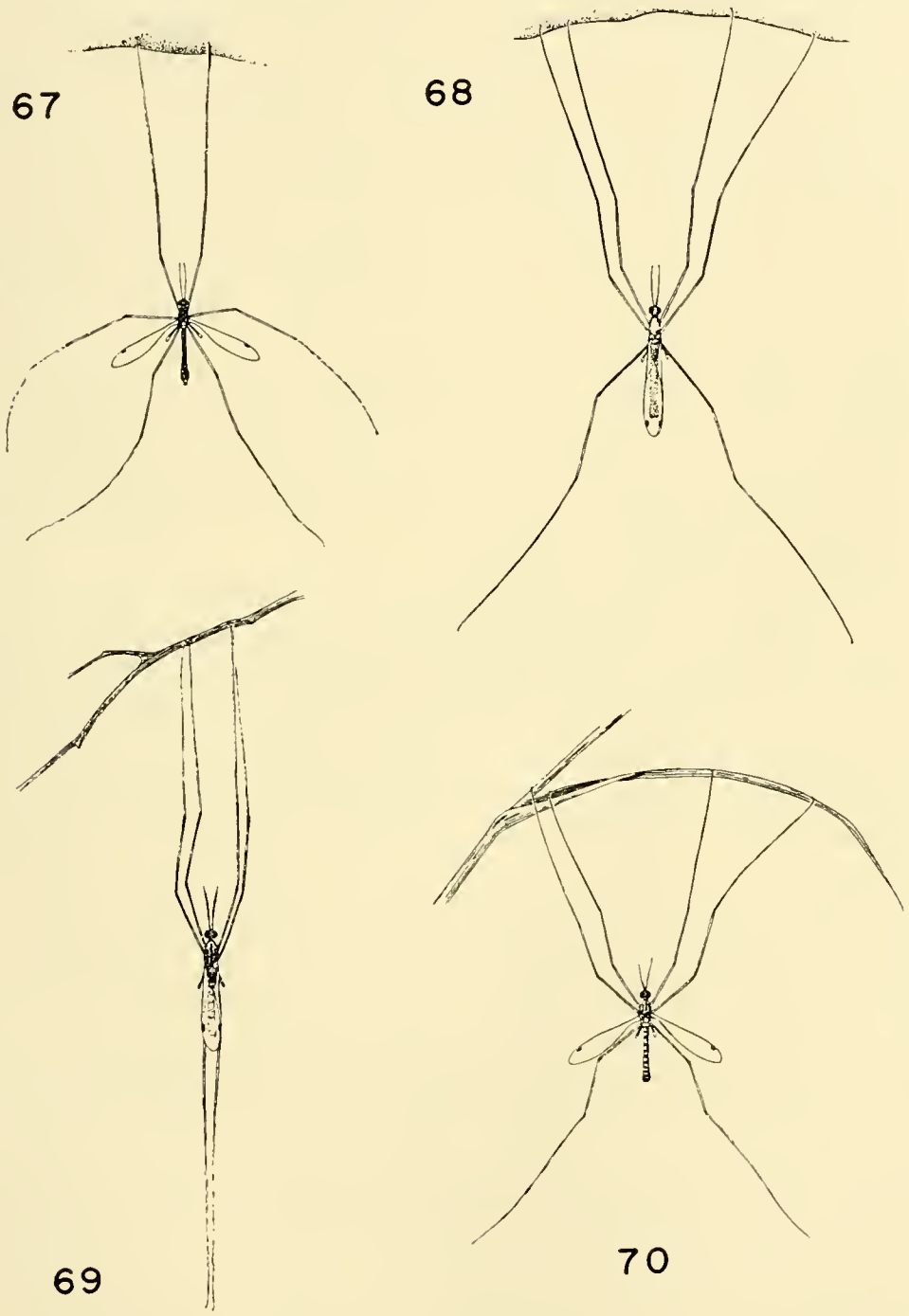


FIG. 67. Resting posture of *Dolichopeza (Dolichopeza) americana.* FIG. 68. Resting posture of *Dolichopeza (Oropeza) polita* ssp. (also of *johnsonella, obscura* and *tridenticulata*). FIG. 69. Resting posture of *Dolichopeza (Oropeza) carolus* (also of *subalbipes, subvenosa* and *venosa*). FIG. 70. Resting posture of *Dolichopeza (Oropeza) sayi* (also of *dorsalis*).

nearly all were suspended by all six legs, whether from an upside-down horizontal surface or on a more or less vertical surface, and whether single individuals or mating pairs. Commenting on this behavioral difference, Alexander (1920: 982) says "the resting positions of *Dolichopeza* are described . . . and the striking dissimilarities to *Oropeza* noted. It may be that *Oropeza* is not so close to *Dolichopeza* as has been believed." Certainly these two subgenera represent distinct natural groups, but the difference in behavior appears to be no more than a consequence of a morphological dissimilarity that is much less remarkable than the difference in genitalia or wing venation. Comparing several specimens each of *D. (D.) americana* and *D. (O.) tridenticulata*, species of about equal size, I found the ratio of the length of the prothoracic leg to that of the mesothoracic leg to be greater in the former species. In both these species (as also in other species of *Oropeza*), the prothoracic legs slightly exceed the length of the second pair, but the difference in total length is perhaps significant. The ratios for *americana* and *tridenticulata* were 30.5:27.9 mm. and 30.7:29.0 mm., respectively, there being a greater difference in *americana* that might explain its peculiar posture.

The position of the wings in repose is of interest, as there is some correlation with the grouping of species on the basis of coloration, noted earlier. It has been stated that *Dolichopeza americana* rests with its wings outspread and that species of the subgenus *Oropeza* fold their wings over the body when at rest. But this is true only in part. *Dolichopeza americana* (Fig. 67) does rest with its wings apart, a posture that is unique among those species preferring the deep shade, but it is my observation that the swamp inhabiting *D. dorsalis* and *sayi* nearly always rest with their wings outspread and tilted somewhat forward, as they hang among the grasses and stems (Fig. 70). *Dolichopeza johnsonella, obscura, polita* sspp., and *tridenticulata*, flies which seek the deepest shade by day, all fold their wings over their backs and rest with the hind legs dangling out to the sides (Fig. 68). *D. walleyi* is also often seen in this position, especially when concealed in dark recesses, but when out among low plants beneath the trees, it often rests with the wings outspread, a peculiar correlation of variable behavior with different environment. *D. similis*, a swamp dweller usually found among low plants, also exhibits considerable variation in wing position when at rest but usually assumes a resting posture like that shown in Figure 68. A most unusual situation in regard to resting posture is that of *Dolichopeza carolus, subal-*

bipes, subvenosa and *venosa*. Morphologically, *subalbipes* belongs to the *obscura* group and the other three species to the *sayi* group, yet in general coloration and size they are very similar. The commonest environment of each is leafy vegetation in damp, shaded places, although usually no more than two of the four species occur together in the same habitat. The resting postures of these very similar species are identical and at the same time different from those of all other North American species of *Dolichopeza*. They hang by the front two pairs of legs, with the wings folded over the body and the hind legs held almost straight downward and quite close together (Fig. 69), a position that conceivably has some camouflaging effect, judging from its occurrence throughout this group of convergent species.

Reaction of resting flies to changes in light intensity has been noted a few times. Rather regular observations were made of adult *Dolichopeza* congregated in a recess in a sandstone cliff at Turkey Run State Park, Parke County, Indiana. In late May, this hole is well shaded through most of the day and often contains as many as three hundred flies of various species. About five o'clock in the afternoon, however, sunlight strikes the sandy floor of the cavity and by reflection somewhat illuminates the roof, causing the resting flies after a time to move. Under such circumstances, they usually retreat deeper into their crannies and in this case crowded into a small adjoining hole that was only about eight inches high, with perhaps two square feet of roof. In this small but dark retreat I once found about two hundred flies, that is, nearly a hundred per square foot of area available for suspension. At other times, I found that when I reflected sunlight into resting sites, species of *Oropeza* reacted readily, while *D. americana* responded slowly or not at all. When the sky becomes dark with clouds, in the daytime, many *Dolichopeza* leave their shaded hiding places and fly about among the low plants of the woods, but I have also noticed that at such times those remaining at rest are less easily disturbed by the presence of humans than at other times. For example, on one dark, cloudy day resting flies showed no reaction to the presence of my hand held only half an inch from them or slowly circled around them. They took flight immediately, however, in response to a slight touch.

Although Dolichopezas rest quietly during the day, they range rather widely by night. Along McCormick's Creek, in Indiana, I have watched *johnsonella* and other species of the *obscura* group, on a June evening, moving from beneath the limestone ledges out

into nearby trees. In the gathering dusk, they could be seen dancing in mid-air among the trees in the ravine and high up on the face of the cliff. At other times and places, I have observed *D. americana* and *polita* ssp. still at rest a few minutes after darkness, but there is every indication that most *Dolichopeza* are away from their daytime haunts during most of the hours of darkness. It is a common thing to find crannies where hundreds of them rest by day to be quite empty after nightfall. At daybreak, along forest trails, one may find the flies making their way back to darkened shelters. In northern Michigan, I have waited beside an empty daytime resting place of *tridenticulata*, in the early morning, and watched the flies returning from all directions as the sun rose. Further evidence of nocturnal wandering by *Dolichopeza* is found in captures of occasional specimens at light traps (notwithstanding their tendency to avoid the brighter light of the sun), or the finding of flies in temporary structures affording shade from the rising sun (such as tents in a campground), in places far from their diurnal haunts. It is possible that during such excursions away from the protection of daytime habitats, individuals are caught up in high winds and carried to other localities, there to establish new populations of the species.

Although the fairly well developed digestive system of the adult *Dolichopeza* suggests that the flies do some feeding during their short existence, I have only once seen one so occupied. This was *Dolichopeza americana*, seen drinking at a shallow pool of seepage water on a mossy, horizontal ledge of sandstone. The fly stooped, somewhat in the manner of a drinking giraffe, with its head down and tail end elevated, its legs rather evenly outspread. I have no idea what natural foods are utilized, but in the laboratory the flies fed upon thin sugar syrup, which was held in shreds of paper tissue hung upon the sides of the cage. Speaking of crane flies generally, Rogers (1933: 30) says, "Nearly all species that have been reared were able to mate and oviposit without food, and, although feeding practically doubles the life of the adults and tends to prolong somewhat the period of oviposition, lack of food does not appear to decrease the number of fertile eggs oviposited." While my records do not show a doubling of adult life time among flies given food, an increased life span is indicated; and I find no effect of food or lack of it on the fertility of eggs or the period of oviposition by female flies in captivity.

Predators and parasites.—There are no specific records, so far as I am aware, of predation on *Dolichopeza* by a vertebrate or large invertebrate, although Alexander (1920: 721 ff.) presents a for-

midable list of known enemies of crane flies generally, many of which are certainly potential and probably actual predators of *Dolichopeza.* While probing the darkened recesses occupied by these flies, I have occasionally encountered a small salamander or a toad; and it is not an uncommon sight to see a large dragon fly working along a cliff, now diving into a shaded niche, now backing out and flying to another. I once found an ant attacking an emerging *Dolichopeza obscura* that was only partly out of its pupal skin. Swamp species of *Dolichopeza* are undoubtedly picked up by foraging birds, especially at times when they constitute a large fraction of the flying insects present.

It has been remarked that some species of *Dolichopeza* have ". . . a notable predilection for resting on spiders' webs." I would rather say that they often find their chosen resting places occupied also by spiders, from whose webs they are able to hang without often becoming entangled. That Dolichopezas do fall prey to web-spinning spiders, as well as to cursorial ones that stalk them in their crannies, is shown by the following list of spiders collected with their prey:

Dolomedes sp. (immature) with *Dolichopeza* (*O.*) *obscura;* Michigan, Cheboygan Co., Douglas Lake, 6 July 1949.

Philodromus marxii Keyserling with *Dolichopeza* (*O.*) *polita;* Illinois, LaSalle Co., Starved Rock State Park, 7 July 1951.

Meta menardi Latreille (immature) with *Dolichopeza* (*O.*) *tridenticulata;* Indiana, Owen Co., McCormick's Creek State Park, 24 June 1950.

Theridion tepidariorum C. Koch with *Dolichopeza* (*O.*) *polita;* Michigan, Eaton Co., Grand Ledge, 16 August 1951 (three flies in one web).

Theridion tepidariorum with *Dolichopeza* (*O.*) *tridenticulata;* Illinois, LaSalle Co., Starved Rock State Park, 7 July 1951.

Theridion tepidariorum (immature) with *Dolichopeza* (*O.*) *johnsonella;* Indiana, Owen Co., McCormick's Creek State Park, 20 July 1951.

Theridiosoma radiosum McCook with *Dolichopeza* (*O.*) *tridenticulata;* Indiana, Owen Co., McCormick's Creek State Park, 12 June 1951.

Theridiosoma radiosum with *Dolichopeza (O.) obscura;* Indiana, Parke Co., Turkey Run State Park, 19 June 1950.

Theridiosoma radiosum with *Dolichopeza* (*O.*) *polita* ssp. and *Dolichopeza* (*O.*) sp.; Indiana, Parke Co., Turkey Run State Park, 11 June 1951 (three records).

Uloborus americanus Walckenaer with *Dolichopeza (O.) tridenticulata;* Iowa, Clayton Co., near Guttenberg, 8 July 1951.

The following portion of a letter from Dr. Willis J. Gertsch, who identified all the spiders, is of interest: "The *Dolomedes* is a three-clawed vagrant spider which ordinarily runs over the ground or low vegetation, most often near water. The *Philodromus* is also a vagrant and may be seen on the ground, but is rather more frequently swept from herbs and shrubs. The remaining species are all sedentary forms. The *Theridion* is the very common cosmo-

politan house spider. The *Theridiosma* spins an unusual orb web and usually is associated with shaded woods. The same is true of *Meta,* also an orb weaver which favors dark woods and is even partial to caves. *Uloborus* is one of the cribellate orb weavers and makes a beautiful horizontal web."

It so happens that all the records above involve flies of the *obscura* group that frequent rocky crevices and crannies. This fact is related partly to the greater ease with which predation is observed in such habitats and partly to my confessed preference for working in these more comfortable places. I have no doubt that the swampland species of *Dolichopeza* have many spider predators also. It should be added that *americana, carolus, walleyi* and *similis* have been found in the webs of spiders, but in these instances I was unable to find the spiders.

While external parasites probably seldom kill a crane fly, they do sometimes cause their host to become shriveled and undersized (Rogers, 1942: 57). All species of *Dolichopeza* are occasionally afflicted with mites, and as many as eight or ten on a fly is a common thing. The heaviest infestation I have found was a group of 98 mites clustered mostly on the abdomen of a male of *Dolichopeza venosa,* taken in Eaton County, Michigan. The mites usually attach to some part of the thorax, often to the abdomen, and rarely to proximal parts of the legs, but I have never found them attached to the head or wings. Two kinds of mites are the most frequent ectoparasites of *Dolichopeza.* One is a plump, reddish or orange colored erythraeid (Acarina: Erythraeidae) of undetermined genus. The other is a somewhat flattened stigmaeid, identified by Dr. Joseph Camin as belonging to the genus *Ledermüilleria* (Acarina: Stigmaeidae). Actually, there may be two species of this genus parasitic on *Dolichopeza,* as those on some flies are of a rusty orange color, while others on other flies are mottled tan or gray. Their body form is depressed, the dorsum broadly curved and the ventral surface slightly concave.

Only one instance of nematode endoparasitism of adult *Dolichopeza* has come to my attention. This was a male of *Dolichopeza tridenticulata,* collected in Shenandoah National Park, Virginia, on 28 June 1958. Although the total body length of the fly was only 11 mm., the nematode measured almost 35 mm. in length. The parasite was looped from end to end of the fly's abdomen four complete lengths, and its head was inserted far into the thorax of its host. In spite of this condition, the fly was taken on the wing,

and its digestive and reproductive organs, on dissection, appeared intact and capable of functioning.

On two occasions, I have found larval Tachinidae endoparasitic in adult *Dolichopeza*. Dissection of the abdomen of a male *Dolichopeza carolus* taken in Neel Gap, Union County, Georgia, 28 June 1952, revealed two small dipterous larvae identified as tachinids. On 6 June 1960, at Cumberland Falls State Park, Whitley County, Kentucky, I captured a female *Dolichopeza tridenticulata* with a peculiarly bulging abdomen. Unfortunately, I did not notice this enlargement until after the fly had been killed in the cyanide jar and the 3.5 mm. long tachinid parasite was forcing its way out of the abdominal cavity through the pleural membrane. Dissection showed the vital organs of the host intact, so it seems likely that the tachinid had fed chiefly on the fat tissue and perhaps the haemolymph.

MATING BEHAVIOR

It is probable that in most species of *Dolichopeza* mating usually occurs during the night, although in certain species pairs are not uncommonly found still in copulation well into the following daylight hours; and occasionally matings are commenced during the day, especially if the light intensity is low, as when the sky grows dark before a summer thunderstorm. As suggested earlier, late evening swarming noted in a few species may be a preliminary to mating, but it is not possible at this time to say what pre-mating activities are typical for the genus under natural conditions. Observation of diurnally mating pairs and those artificially illuminated in the laboratory provides the only exact information on mating behavior, the basis of the following descriptive comments.

Attracted to the same shaded daytime resting sites, males and females are brought into close proximity but appear to ignore one another unless actual physical contact, usually of tarsi, occurs. Now and then, when a resting group of flies is disturbed and is set into dancing motion, a male may attempt copulation with one or more females before settling to rest again. Unreceptive females, in the case of *Dolichopeza polita* ssp., have been seen to respond to these attentions by fluttering their wings and kicking their hind legs over their backs. If a female is receptive, however, she moves her wings slightly apart and remains quietly suspended, while the male hovers over her, curves his abdomen down alongside hers, and reaches from below or behind to gain a grip upon the ovipositor with his dististyles (Fig. 71). I have observed these reactions, with minor variations, also in *Dolichopeza americana, sayi, tridenticulata*

and *walleyi* and suspect that they are rather uniform throughout the genus.

During copulation, the female ordinarily supports the weight of both flies, as the male hangs head downward, held fast by the grip of his genital appendages (Fig. 72). Seen from the side, the legs of the flies are not arranged generally in one plane as they might seem from the figure. The fore and hind legs of the male are held out somewhat dorsally with respect to the fly's body and the mesothoracic legs somewhat ventrally. The hind legs of the female (and the middle legs, in the case of *americana*) are deflected in a similar manner. In *americana,* the wings of both partners are held out to the side, but in *Oropeza* spp. the female normally keeps her wings folded over her back, while the male holds his wings outspread. Because of the manner of coupling, suspended mating pairs are so oriented that the dorsal surface of the male and the ventral surface of the female face the same direction. If both members of the pair are clinging to some support, as often happens, their abdomens are variously revolved to maintain the proper clasp. Each may rotate the abdomen 90 degrees, or one may twist 180 degrees, etc.

The following is the usual arrangement of the copulatory structures in mating: The male grasps the female genital segments from below or behind, his outer dististyles getting a loose hold about the tenth tergum. When the hypovalves of the female have been maneuvered into the male's genital chamber, he closes the tips of the inner dististyles into sclerotized folds on the dorsal or inner surfaces of the hypovalves. This provides the firm grasp that is so strong as to allow mating pairs to take to the wing, when alarmed, and not become separated. It may be seen in Figure 73 that the pressure of the tergal arms on the edges of the hypovalves serves to brace them securely against the underside of the ninth tergum of the male, while the gonapophyses force the tenth tergum and cerci apart from the hypovalves. This wide separation of upper and lower elements of the ovipositor exposes the opening to the bursa copulatrix, into which the penis is inserted, as indicated by dotted lines in Figure 73. In *Dolichopeza americana,* the absence of tergal arms seems compensated by a shift dorsad in the position of the inner dististyles, which hold the hypovalves well apart from the cerci. The specific configuration of the medio-posterior margin of the ninth tergum of the male does not seem to have any functional significance.

Although I have never observed males waiting beside female pupae, as described by Alexander (1919: 881) for several other

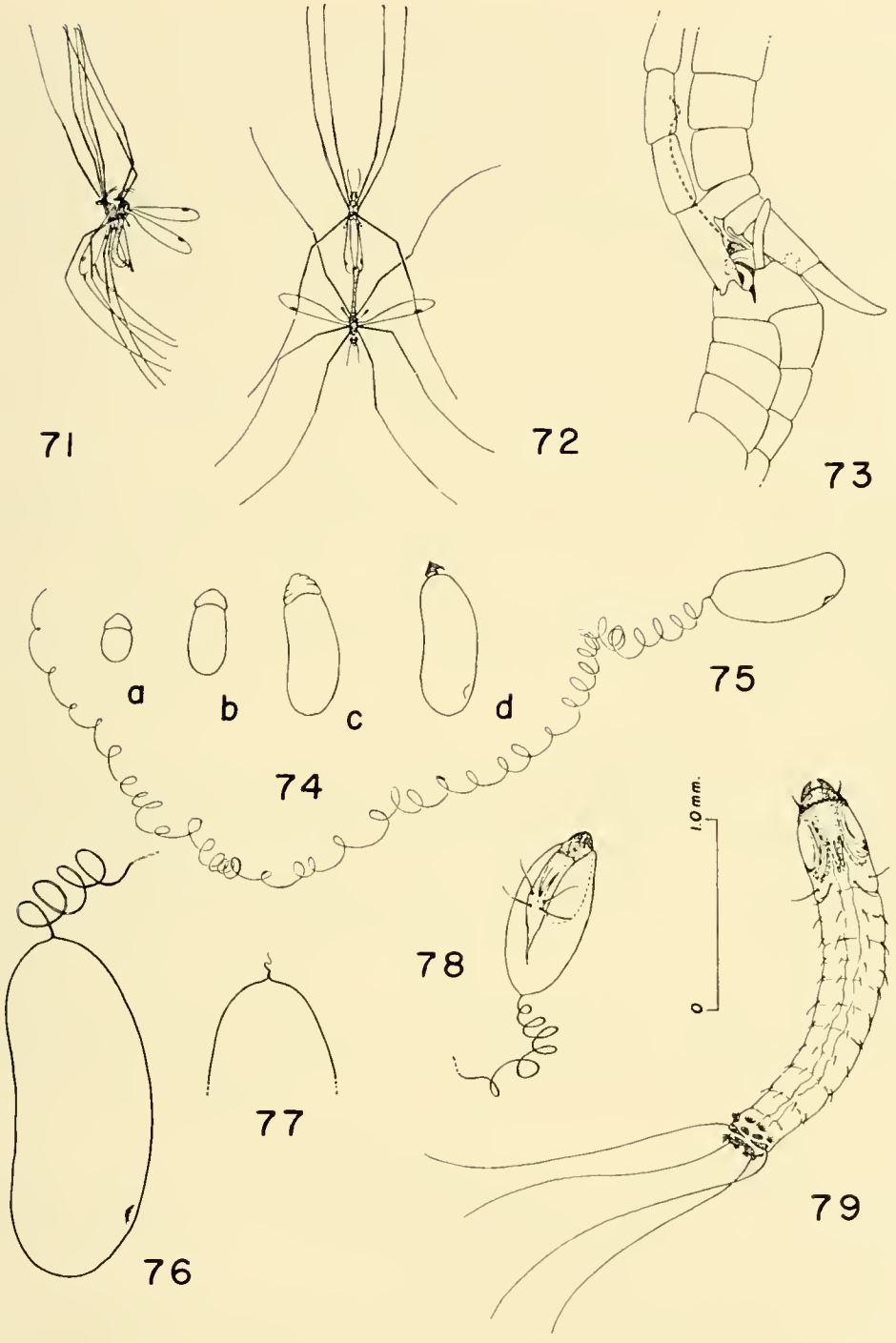


FIG. 71. Position of male (shaded) and female (not shaded) *Dolichopeza (Oropeza)* sp. preliminary to mating. FIG. 72. Same as 71 but showing position in mating. FIG. 73. Detail of hypopygia of male and female *Dolichopeza (Oropeza)* sp. in mating. FIG. 74. Stages in development of egg of *Dolichopeza (Oropeza)* sp.; a-c—immature eggs, showing cap of cells from which terminal filament develops, d—mature egg, showing coiled terminal filament. FIG. 75. Egg of *Dolichopeza (Oropeza)* sp. with terminal filament uncoiled. FIG. 76 same as 75, enlarged, showing micropyle. FIG. 77. Egg of *Dolichopeza (Oropeza) polita polita*, showing vestigial terminal filament. FIG. 78. Hatching of egg of *Dolichopeza (Oropeza)* sp. (scale pertains to Figs. 78 and 79 only). FIG. 79. Larva of *Dolichopeza (Oropeza) obscura*, first instar, 48 hours after emergence from egg.

genera, I do believe that females are somehow found by males and mated with very soon after emergence. Mating pairs frequently involve teneral females whose abdomens are still soft and show the greenish color of the immature stages. As emergence almost always occurs during the hours of night, it is somewhat of a problem to understand just how males and females come together (compare with above description of daytime mating activities). To learn more about nocturnal behavior of these flies, I have made many trips to known larval and pupal habitats, and, using an electric lantern, watched for emergence and subsequent mating. In no case did I find mating to take place near the pupal site, so I assume that some amount of flight is involved in bringing the two sexes together. Mating appears to take place usually at some distance from diurnal resting sites, for these are nearly always vacant at night. In northern Michigan and in Indiana, however, I have found many mating pairs of *Dolichopeza tridenticulata* beneath the eaves of sheds, at about midnight, where earlier in the day only single flies could be found.

In dimly-lit rock gorges and other similar places, one may find mating pairs, here and there, nearly any time of day, in season; but almost all pairs of the majority of species were observed to separate by mid-morning. Mating pairs of *americana* and *polita* sspp., however, are often found during the daylight hours. In Clifty Ravine, Jefferson County, Indiana, on 3 August, I found hundreds of mating pairs of *americana*, at nine o'clock in the morning, when the hazy sunlight had not yet become bright through the trees. Almost no unmated individuals were seen. This same situation was found again, about noon of the same day, in Muscatatuck State Park, Jennings County, Indiana. At Nelson Ledges State Park, Portage County, Ohio, dozens of mating pairs of *polita* sspp. were collected in the hour just before noon on 14 July.

The duration of mating is not known, but the pairs of *americana* and *polita* mentioned seemed to have been formed during the previous night, that is to say at least six to eight hours before the time of observation. In the laboratory, pairs of *walleyi* and *sayi* remained in copulation for as long as eight hours, and under natural conditions a pair of *tridenticulata* was observed together at sunrise and for three hours thereafter.

It is probable that mating takes place throughout the egg-laying period, which lasts about three or four days, perhaps longer in some females. When flies were confined to close quarters in the laboratory, mating sometimes occurred on three successive nights.

Females from mating pairs collected in the field frequently are found to contain only a few eggs, suggesting at least one prior mating.

It would seem that among closely-related species living so near to one another that there might occur frequent matings or attempted matings in which the partners are of different species. However, I have never observed this to happen. Among many hundreds of mating pairs observed or collected, not one was found to involve two species. A male of *Dolichopeza carolus* was once found apparently attempting to gain a copulatory hold on a female of *americana* that was already mated with a male of her own species; and I have seen, in dense, dancing swarms of several species, males very briefly approaching females of another species but never going so far as to secure a grasp with the hypopygium. It is understandable that size differences would serve as a barrier to cross-mating, in some cases, as between males of *polita* and females of *americana* often found sharing the same resting sites. But among adults of many other species that come into actual contact or near contact there are no such obvious barriers to cross-mating. The genitalial clasp is general in nature, far from the complex "lock and key" interrelationship described for some insects, and appears to be essentially the same among many species observed. But it is more significant that cross-matings seem in general not even to be attempted. Accordingly, it must be that by means of some sense as yet unknown the flies are attracted to mates of their own kind and either repelled or at least not attracted by other species, no matter how closely the two may apparently be related.

OVIPOSITION

In the laboratory, oviposition occurred almost without exception during the night and was never observed by day. Neither have I ever seen females of *Dolichopeza* in their natural surroundings behaving during daylight hours as if they were laying eggs. However, on a few occasions females of *polita, tridenticulata* and *walleyi* were seen ovipositing during late evening, just before the dark of night. These females were flitting up and down cliff faces, flying very close to the thin carpet of mosses that covered the rock. After a time of seemingly random movement (it is possible certain mosses were being sought), a given female fly would commence a series of bouncing motions over an area of moss perhaps four inches in diameter. The bouncing action is accomplished by rapidly alighting on the tips of the tarsi, flexing the legs slightly, and pushing off into

flight once more, the wings vibrating all the while. As the fly thus bounces, at about 90 times per minute, it occasionally and quite suddenly thrusts the tip of the abdomen deeply into the moss, withdrawing it almost immediately. The fly may repeat this motion as many as 25 or 30 times before departing to another place.

The activity associated with oviposition in these three species was quite uniform, and it therefore seems that it may be rather similar in the other species, allowing of course for some modification due to differences in the kind of habitat, as for example whether the moss surfaces are vertical or horizontal. In the mosses, the eggs are found to be laid singly but several in a small area; that is, while several may be found within a space an inch in diameter, they do not occur in any sort of cluster, such as has been described for some other Tipulinae. In the laboratory, also, eggs are deposited singly, except when the available substrate is so limited as to force females to lay their eggs in groups.

EGGS

Matured eggs of all species of North American *Dolichopeza* have the same general appearance: oblong, slightly narrower at the posterior end, and with a chorion of intense black color, with a bluish or purplish, almost metallic sheen. The chorion is so smooth that at more than 200 × magnification there is no indication whatsoever of any surface sculpture. The position of the micropyle is indicated by an indentation of the chorion on the ventral surface, near the anterior end (Fig. 76). Orientation of the egg is based upon the usual position of the larva at the time of hatching.

Within the ovarioles, the developing eggs appear as buff colored, granular, oblong bodies. The smooth chorion is found only on those eggs which have moved into the lateral oviducts or are in the extreme lower ends of the ovarioles. Pale colored at the time of emergence of the adult female, the eggs soon darken, so that in a female only a few hours old the lateral oviducts are bulging with black masses of fully-formed eggs, all lying more or less horizontally, with their posterior ends directed towards the gonopore.

Eggs of some species of *Dolichopeza* bear a terminal filament of great length, the function of which seems to be retention of the egg in the moss where it is laid. This structure originates from a whitish cap of cells upon the end of the developing egg (Fig. 74) and by the time of oviposition has the form of a springlike, broadly conical, tight coil. Drawn out to its full length, it is seen to be from

ten to fifteen times the length of the egg itself. I have not been able to correlate the presence or absence of the terminal filament with either the type of larval habitat or the phylogenetic affinities of the species. It is present in *Dolichopeza americana,* in *johnsonella, obscura* and *tridenticulata* of the *obscura* group, and in *sayi* of the *sayi* group. It is totally absent in *subalbipes* of the *obscura* group, and in *carolus, dorsalis, similis, subvenosa, venosa* and *walleyi* of the *sayi* group. Curiously, in all three races of *polita* it is present in a very rudimentary form, although recognizably different in each subspecies. In the typical subspecies (Fig. 77) the filament usually forms one open coil or loop; in the western subspecies it has the shape of a hook and never forms a complete coil; and in the central race it forms one or two irregular coils in a plane perpendicular to the basal part of the filament.

In attempting to find out what numbers of eggs are laid (or are probably laid) by the various species, I have dissected females that were collected into alcohol at a time when they seemed to be still rather teneral and quite filled with eggs, even into the first abdominal segment. In such females, it is difficult to imagine where more eggs would be placed if there were any more, so the count of matured and nearly matured eggs present was taken as the number which the fly would probably have oviposited. In nearly-spent females, perhaps only one or two matured eggs may be found in the oviducts, while the very much undeveloped eggs in the ovarioles are still in place. Thus, there seems not to be a continuing development of eggs throughout the period of oviposition, but rather a brief initial period of maturing of all those eggs which are going to be laid at all. Egg counts in females of several species from different parts of the country are surprisingly constant, varying in the vicinity of 100 to 140, depending on the species. Rogers (1933: 32) gives the number of eggs actually laid as 250 to 350 for the Tipulinae in general, and, in an unpublished paper, the numbers 200 and 250, more or less, for two individuals of *Dolichopeza obscura* from Florida. However, my examination of another Florida female of *obscura,* in which all eggs seemed to be still in place, revealed 104 eggs in advanced stages of maturity and no more than three dozen countable eggs in the ovarioles. A very teneral female *tridenticulata* from Jefferson County, Indiana, contained 90 fairly darkened eggs and about 50 in various developmental stages. From a female *americana,* 106 matured eggs were taken, and there were not many others that looked as if they might eventually have

been laid. From all the indications available to me, I would estimate the potential egg production of an average female of *Dolichopeza* to be about 120 eggs.

Dimensions of the eggs vary somewhat proportionally with the body size of the individual female and only very generally with the average body size of the species. The smallest eggs measured were of the small species, *Dolichopeza americana* and *tridenticulata*, while the largest eggs found were those of *similis*, the largest *Dolichopeza*. Average dimensions of eggs from average sized females were:

americana—.60 x .25 mm.
carolus—.79 x .37 mm.
dorsalis—.76 x .31 mm.
johnsonella—.74 x .29 mm.
obscura—.73 x .40 mm.
polita ssp.—.75 x .30 mm.
sayi—.72 x .31 mm.
similis—.92 x .35 mm.
subalbipes—.83 x .36 mm.
subvenosa—.75 x .31 mm.
tridenticulata—.65 x .30 mm.
venosa—.79 x .32 mm.
walleyi—.76 x .32 mm.

Measurements were made with a camera lucida scale from eggs mounted on slides. Because the eggs are likely to be somewhat flattened when so mounted, the widths given here are subject to slight error.

Duration of the egg stage in *Dolichopeza* has been reported only once (Rogers, 1933: 32), the time given being 13 to 16 days, for *D. obscura* at outdoor temperatures in March and April, in Florida. However, among several groups of eggs kept at both room and outdoor temperatures, in Indiana, Michigan and Minnesota, I have found the time to be closer to eight days. My observations are summarized in Table 2.

TABLE 2.—Duration of the Egg Stage in Some Species of North American *Dolichopeza*

Species	Date of hatching	Duration of egg stage	Where kept
americana	19 Aug.	7-8 days	laboratory
carolus	24 June	9 days	outdoors (Indiana)
dorsalis	22 July	9 days	outdoors (Minnesota)
johnsonella	29 June	8-9 days	outdoors (Indiana)
obscura	2 Aug.?	10 days?	laboratory
polita ssp.	24 Aug.	7-8 days	laboratory
polita ssp.	6 Sept.	7-8 days	laboratory
sayi	6 Sept.	6-7 days	laboratory
sayi	26 Sept.	7 days	laboratory
similis	25 June	7 days	laboratory
venosa	8 June	7 days	laboratory
walleyi	9 June	7-8 days	laboratory

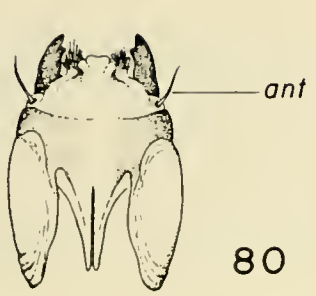
Durations are given from time of oviposition to date of abundant hatching. Where the length of the egg stage is indicated as uncertain, the date of oviposition of the first eggs to hatch is not known but is one of two known dates. It will be noted that outdoor times are in all cases the longer, except for *obscura*, which was in an unheated building in the woods of northern Michigan. Laboratory or room temperatures seem to accelerate development by about one day.

LARVAE—MORPHOLOGY

First instar larva.—As it comes from the egg, the larva of *Dolichopeza* seems to be mostly head capsule and caudal setae (Fig. 78); the body is extremely short and transparent, and only the tips of the mandibles are at all strongly sclerotized. Within three or four hours after hatching, however, the larva stretches out to somewhat less than two millimeters in length, exclusive of the caudal setae, and the head capsule, darkened to a grayish color, becomes discernible in some detail. At first nearly rectangular in outline when seen from above, the head assumes its more oval shape in about a day. The integument of the very young larva becomes a dirty yellowish color, yet is transparent enough that the viscera show clearly through it; and it bears an inconspicuous covering of extremely minute hairs, in addition to the weak bristles indicated in Figure 79.

There are several details in which the head of the first instar larva (Fig. 80) differs markedly from that of later instars. Perhaps the most conspicuous of these is the antennal structure. In later instars, the antennae are cylindrical, with an apical sensory peg, but in the first instar they are setiform. The fronto-clypeal plate is relatively larger, and the backward extensions of the lateral plates that parallel it in later instars are absent in the very young larva. Although not studied in more than a few species, the mandibles, mentum and hypopharynx generally have fewer and more rounded teeth than their counterparts in the more mature larva. In the heavily sclerotized head capsules of older larvae, I had long overlooked the eyes, but their position in the first instar larva is clearly indicated by concentrated spots of violet-purple pigment similar in color to that associated with the compound eyes of the adult flies.

The spiracular disc of the first instar larva contrasts even more remarkably with those of all subsequent instars; in fact, except for the presence of spiracles, it has almost no characteristics in common with them. Below the spiracular openings are four sclerotized



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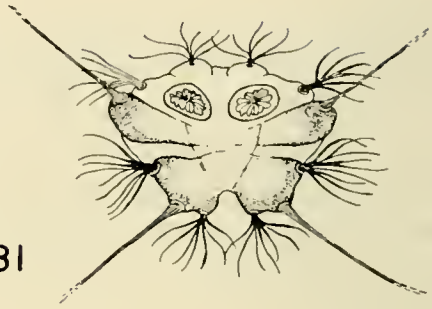

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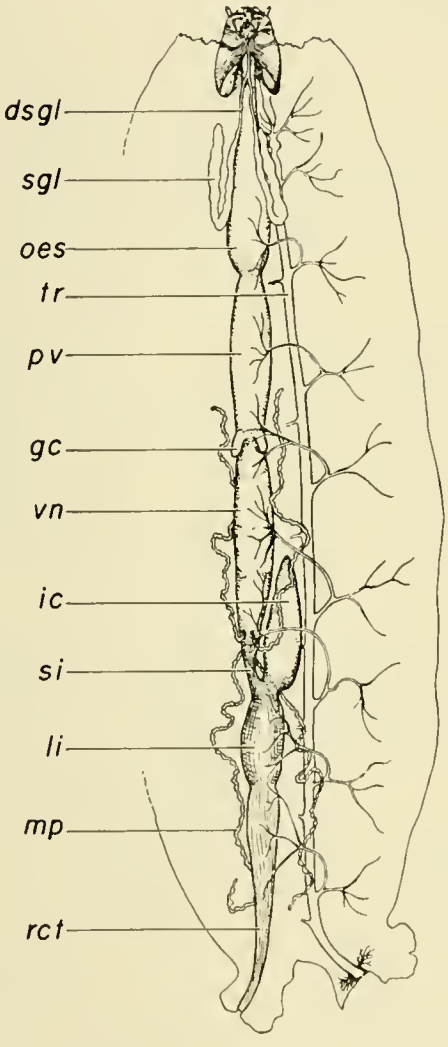

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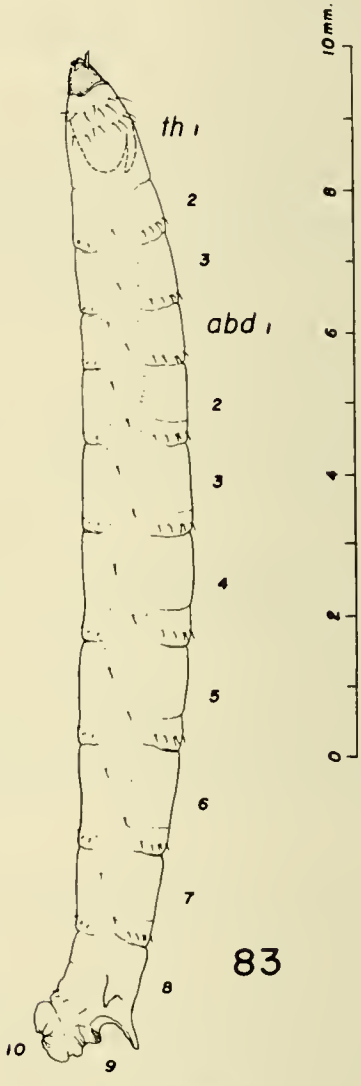

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FIG. 80. Head capsule of first instar larva of *Dolichopeza (Oropeza)* sp.; ant—antenna. FIG. 81. Spiracular disc and associated structures of first instar larva of *Dolichopeza (Oropeza) obscura.* FIG. 82. Gross internal anatomy, digestive and respiratory systems only, of fourth instar larva of *Dolichopeza (Oropeza) obscura;* dsgl—duct of salivary gland, gc—gastric caecum, ic—intestinal caecum, li—large intestine, mp—Malpighian tubule, oes—oesophagus, pv—proventriculus, rct—rectum, sgl—salivary gland, si—small intestine, tr—trachea, vn—ventriculus. FIG. 83. Fourth instar larva of *Dolichopeza (Oropeza) obscura,* indicating thoracic and abdominal segmentation; th—thorax, abd—abdomen.

plates, a dorsal pair narrowly fused at the midline and a ventral pair of broader plates, the medial borders of which are indistinct. Each of these plates bears a long, slender caudal seta on its distal margin (Figs. 79 and 81). Across the top of the spiracular disc are four broadly-rounded, low protuberances, each with a tuft of bristles at its apex. Two similar tufts of bristles are borne on each of the ventral plates, in the positions shown in Figure 81. It is difficult to homologize these various structures with those seen on the spiracular disc of the older larva. However, it seems not unlikely that the four dorsal protuberances correspond to the four conical dorsal lobes found in the same position in the later instars. Either pair of sclerotized plates may be homologous with sclerotized, bristle-bearing areas of relatively much smaller extent on the ventral lobes of the spiracular disc of the more mature larva; but I am more inclined to believe that it is the lower pair, which means the upper pair has no counterpart in the older larva. The general similarity of the spiracular disc of the very young *Dolichopeza* larva to that of the later stage larvae of some Limoniinae (such as *Limnophila* and *Pseudolimnophila*) is striking. The very long caudal setae and tufts of bristles possibly serve to hold the respiratory openings above the water surface in case the larval habitat becomes saturated. Similar structures are found in the first instar as well as later stage larvae of the more aquatic relatives of *Dolichopeza*, such as *Megistocera* (Rogers, 1949:9); therefore, it may be that these bristles and setae have no function in *Dolichopeza* but are merely rudiments inherited from ancestors that lived in wetter habitats. I have observed that some larvae lose part or all of one or more caudal setae and apparently are none the worse for it. With the first molt, the tufts of bristles and the sclerotized plates and their setae are all lost.

Fourth instar larva.—Larvae in the second, third and fourth instars differ mostly in size and are so similar in structure that a description of the last will suffice for all. The body is elongate, nearly terete but slightly depressed, thickest at mid-length, tapering rather evenly and gradually toward both ends, 12 to 18 millimeters in length and about two millimeters in breadth, depending on the species. The skin is thin and soft but tough. It is covered by extremely small patches and rows of microscopic hairs, variously arranged according to the species. In most species, there are also transverse ridges of larger hairs on both the dorsal and ventral surfaces but more distinctly developed on the dorsum.

The body of the larva consists of a strongly sclerotized, oval, depressed head capsule, three "thoracic" segments and ten "abdominal" segments, of which all are rather easily distinguishable except the last two (Fig. 83). Heretofore, the region I have designated the ninth and tenth abdominal segments has been considered a single segment (Wardle, 1926:29) but may comprise the ninth through eleventh morphological segments, while that which I have indicated as the prothorax has been regarded as two segments, probably because it bears two rows of bristles instead of the single row found on most other segments. The interpretation of segmentation presented here is based upon studies of the internal as well as external anatomy of the larva and upon correlation of larval structures with those of the pupal and adult stages.

Head and mouthparts.—Since virtually the only larval structures that are strongly sclerotized, hence of fixed size and shape, are associated with the head, this part of the larva has been studied in considerable detail by earlier investigators. Thus, Alexander (1920:983) gives a rather detailed descriptive paragraph on the head and mouthparts of the larva of *Dolichopeza tridenticulata* (as *Oropeza obscura*), the only North American species concerning which there are any published morphological data. The head has the characteristic tipuline appearance. Its sides are formed by the large lateral plates, which by their oval outline, striated pattern and concavo-convex shape somewhat suggest deep clam shells. Cook (1949:8) regarded these lateral plates as belonging to the maxillary segment of the head, in *Holorusia*, but I cannot accept such an interpretation in the case of *Dolichopeza*. That the muscles of the mandibles and maxillae originate on the lateral plates suggests rather that these plates are homologous with the vertex of the ocular segment, as in so many other kinds of larvae.

Ventrally, the lateral plates are separated by a somewhat triangular space (Fig. 84), but dorsally they fuse with the narrowly triangular fronto-clypeus (Fig. 85, fclp) along much of its length. From the dorsal margin of each lateral plate, a bladelike projection extends backward alongside the frontoclypeus, slightly exceeding the posterior end of the lateral plate in species of *Oropeza* but conspicuously longer in the subgenus *Dolichopeza*. The sclerite I have designated as the fronto-clypeus has been called the epicranial plate by Comstock and Kellogg (1902) and the clypeus by Cook (1949), who so identified it by the fact that the muscles of the cibarium originate on it. However, the dorsal muscles of the

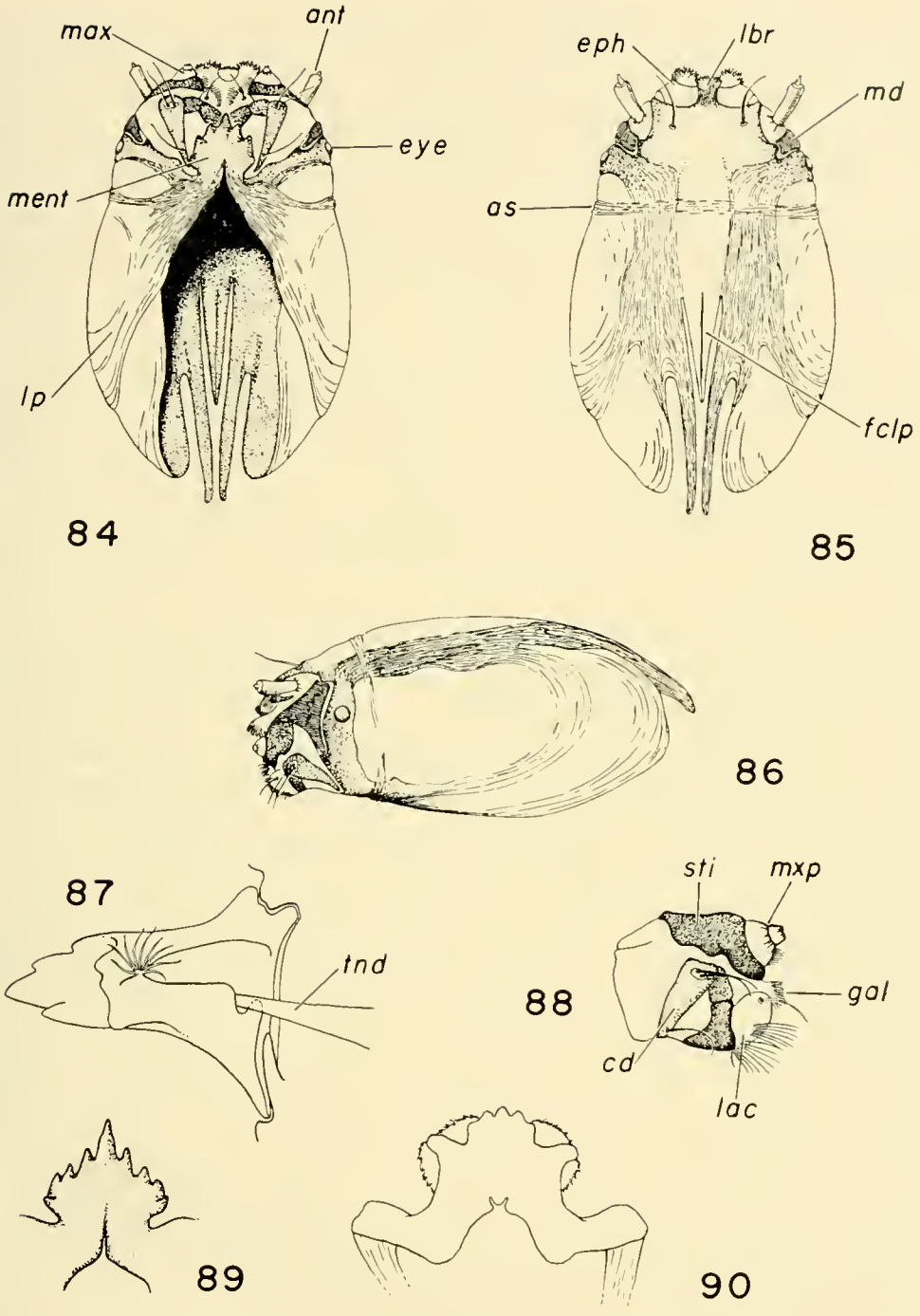


FIG. 84. Head capsule of fourth instar larva of *Dolichopeza (Oropeza) obscura*, ventral aspect; ant—antenna, lp—lateral plate, max—maxilla, ment—mentum. FIG. 85. Same as 84, dorsal aspect; as—line of attachment of skin, eph—epipharynx, fclp—fronto-clypeus, lbr—labrum, md—mandible. FIG. 86. Same as 84, left lateral aspect. FIG. 87. Right mandible of fourth instar larva of *Dolichopeza (Oropeza) similis*, mesial aspect; tnd—tendon of adductor muscles of mandible. FIG. 88. Right maxilla of fourth instar larva of *Dolichopeza (Oropeza) obscura*, ventrolateral aspect; cd—cardo, gal—galea, lac—lacinia, mxp—maxillary palp, sti—stipes. FIG. 89. Mentum of *Dolichopeza (Oropeza) similis*, ventral aspect. FIG. 90. Hypopharynx of *Dolichopeza (Oropeza) dorsalis*, ventral aspect.

pharynx, which typically have their origin on the front, also originate on this same sclerite, which is why I regard it as the fronto-clypeus. A zone of fine wrinkles girdles the entire head at the line of attachment of the skin. The fronto-clypeus joins the labrum almost imperceptibly. A large bristle, subequal in length to the antenna, is borne near the middle of each side of the labrum, and a narrow, medial projection from the anterior margin of the labrum appears to bisect the broad, brushy epipharynx, to which it is immovably joined. The antennae consist of a cylindrical basal segment about four times as long as thick and an apical sensory peg. They are attached to membranous areas at either side of the labrum. Below the labrum-epipharynx are the mandibles, each of which articulates on a blunt dorsal condyle at the junction of the lateral edge of the labrum with the lateral plate and an elongate ventral one on the mid-anterior edge of the lateral plate (Figs. 86, 87). The mandible has four marginal teeth (rarely five) and a broad, inner molar protuberance having somewhat the form of a ridge across the mandible. Behind this molar ridge is an excavation within which is attached the tendon of the adductor muscle of the mandible and at the distal end of which is situated a small tuft of bristles. This tuft has been called the brustia; its function is unknown to me. Attached below the mandibles but overlapping them apically are the subrectangular maxillae. The maxilla (Fig. 88) comprises a narrowly triangular cardo bearing three long setae, an irregularly shaped and very heavily sclerotized stipes, a blunt maxillary palp, and the indistinctly differentiated, apically hairy galea and lacinia, the latter more ventral in position. The mouth cavity is closed ventrally by the mentum, a structure formed by the fusion of forward extensions of the lateral plates (Fig. 84). In some species, particularly in the *obscura* group, the mentum usually has only five rather blunt teeth, but in others (as *D. similis*, Fig. 89) they number seven and are more acute. In all species, there is in addition a small lateral tubercle at each side of the base of the mentum. Just dorsal to the mentum, within the mouth cavity, is the hypopharynx, into which the salivary duct empties. Its upper part is weakly sclerotized and covered with hairs, but the lower portion is strongly sclerotized and bears usually three blunt teeth (Fig. 90). The shapes of the hypopharynx and mentum, specifically of their toothed margins, have been found of limited use in the recognition of species.

Since larvae of *Dolichopeza* are sensitive to light, it seems only reasonable to suspect that they have eyes of some sort, which they

do. The eyes consist externally of a single, circular, only slightly protruding ocellus. They are situated one at either side of the head, in the foremost part of the lateral plate, just behind the mandible (Fig. 86). As the pigmented portion of the eye behind the hyaline lens is dark, the eyes are well concealed in the densely sclerotized walls of the head. Probably all crane fly larvae have eyes, but references to their existence in the larvae of the subfamily Tipulinae are rare. Peterson (1951: 256) probably was referring to species of the Limoniinae when he wrote "ocelli . . . may occur adjacent to the mandibles." At any rate, his figure C, page 279, shows no eyes in *Tipula abdominalis*. Cook (1949), in a detailed study of the head capsule of *Holorusia rubiginosa*, noted the presence of eyes in that species; but most authors, less attentive to detail, have generally overlooked them throughout the Tipulinae, Comstock and Kellogg having failed to observe them even in *Holorusia rubiginosa*, a species they described in detail. In the less strongly sclerotized head capsules of some Limoniinae, such as *Pedicia* and *Dicranota*, the eyes are more easily seen but still have been referred to only cautiously as "eye spots" (Miall, 1893: 237 and plate I; Alexander, 1920: 1092, plate LXI).

Caudal segments.—On comparing genera of larval crane flies, one's attention is almost invariably drawn first to the spiracular disc, which is the area surrounding the two large spiracles on the ninth abdominal segment. This ordinarily well-exposed surface usually exhibits great differences from genus to genus and often easily noticeable differences among species within a large genus. Within groups of closely related species such as North American *Dolichopeza*, however, there is considerable uniformity in the appearance of the spiracular disc and its surrounding structures. In larvae of *Dolichopeza*, the spiracular disc is generally devoid of hairs but has three pairs of small, darkly sclerotized plates disposed around the spiracles as shown in Figure 92. Just below the disc are two broad, rounded lobes, each having a sclerotized apex from which extends a weak bristle. Other bristles occur on the sides of these lobes as shown. Above the disc are the more or less conical, fleshy lobes to which reference has already been made in the discussion of the first instar larva. These four lobes are, in one form or another, characteristic of all species of Tipulinae, although the belief that there were only three dorsal lobes in *Dolichopeza* s. s., as first described by Beling (1886: 190), has persisted almost to the present day (for example, see Hennig, 1950: 396). Beling

stated that, of the usual four lobes above the spiracular disc in larval tipulines, the middle two in *Dolichopeza albipes* of Europe are grown together. Since Beling's time, several authors have commented on this condition, it being unique among all Tipulinae. When I first found the larva of *Dolichopeza americana,* in the winter of 1949, I noted that the apparently single median lobe was actually formed of two lobes closely appressed and that the two separated easily at the light touch of a needle. It seemed that the same might be true of *D. albipes,* but it was not until 1955 that I was able to verify this by examination of specimens in the British Museum. Only once among several hundred larvae examined have I found an instance of true complete fusion of the middle lobes. This was in a fourth instar larva of *D. sayi,* which in the third instar had been quite normal (see Fig. 39). This unusual specimen was preserved because of its singularity.

Situated dorsolaterally on each side of the eighth abdominal segment of larvae of the subgenus *Oropeza* is a subconical lobe (Fig. 92), similar in texture and often in size to the outer lobes above the spiracular disc. These lobes are characteristic of *Oropeza* but are also found in at least one other subgenus, *Trichodolichopeza,* or at least in the only two species, *hirtipennis* and *flavifrons* of South Africa, known in the larval stage (Wood, 1952: 88). Absence of such lobes on the sides of the eighth abdominal segment in the subgenus *Dolichopeza* (Fig. 91) gives those larvae somewhat the appearance of larvae of *Tipula,* but the green color and peculiar markings of the dorsum (Fig. 97) are different from any *Tipula* known to me and should make differentiation easy.

The tenth abdominal segment, or anal segment, is located ventrally with respect to the ninth and comprises four blunt, pale, membranous lobes surrounding the anus. There is no doubt that these lobes are homologous with the anal gills developed in many species of Tipulinae as well as rather generally in the family; however, as they appear on dissection to have no respiratory function (as discussed below), I shall refer to them merely as anal lobes. There are a supra-anal or posterior pair and a sub-anal pair.

Integument.—The soft but tough larval skin bears two size categories of microscopic hairs, in addition to the macroscopic setae (which are the same in all species). As the hair patterns of the dorsum and venter are in general similar, although much less well developed on the underside of the body, a description applying in detail only to the dorsum follows. Seen by the unaided eye or only slightly magnified, the larva of *Dolichopeza* appears to have many

darkened, transverse ridges on its back. In some species, these occur six or seven (rarely eight) per body segment, except where they are obscurely merged on the thorax and on the eighth abdominal segment; but in other species it is difficult to discern separate ridges at all, due to their irregular distribution. Using magnifications near 30 or 40 ×, the transverse ridges are seen to be formed of rows of hairs (Fig. 94). These, the larger of the two sizes of microscopic hairs, are many times as long as they are in diameter. The other size referred to are extremely short and appear to be no more than tiny spots, except at very high magnifications. At medium magnifications, rows of these minute hairs look like short, dark lines in the areas between transverse ridges and oriented more or less parallel to the ridges; but at high magnifications (60 to 80 ×) they may be seen as individual, short hairs, arranged in short or long rows (Figs. 95, 96). On the pleura the minute hairs may be arranged in rather circular patches or may occur singly, while the longer hairs are absent. As the pattern of distribution of these two kinds of integumental hairs seems to be fairly constant for a species, I have made extensive use of it in the key that follows this section.

Internal anatomy.—The internal structure of larvae of *Dolichopeza* was examined only in a general way, in an attempt to find specific or group characters for taxonomic use, but the anatomy of all species studied was found to be rather uniform. Only the digestive, tracheal and nervous systems are discussed here. The sketch of the internal organs (Fig. 82) was made from a larva killed by immersion in boiling water, which accounts for the outstretched condition of all the viscera. In living larvae or those killed by means other than heat, the organs are shorter, broader and not so linearly arranged. The body cavity, especially posteriorly from about mid-length of the ventriculus, is largely occupied by a whitish or light gray perforated sheet of adipose tissue.

Digestive system.—Most conspicuous of the internal structures are the organs of the digestive tract. The oesophagus is a muscular tube, often enlarged at its posterior end. At either side of it lie the whitish-hyaline salivary glands, shown in Figure 82 with a single curve at about their mid-length, although they sometimes are doubly convoluted. Each salivary gland has a narrow lumen surrounded by a secretory portion made up of a single layer of large, cuboidal cells which have correspondingly large central nuclei containing long and much intertwined chromosomes. The chromosomes were not examined in detail. The salivary glands are par-

tially invested with adipose tissue, especially apically, and are drained by slender salivary ducts which unite beneath the oesophagus just within the head capsule. Separated from the oesophagus by a slight constriction is the proventriculus, which in turn empties into the thick-walled, muscular ventriculus. Two short, glistening, pocket-like gastric caeca are appended to each side of the anterior end of the ventriculus, and its posterior end is marked by the attachment of four Malpighian tubules, beaded in appearance except for their nearly-transparent proximal ends, and similarly arranged two at each side of the ventriculus. A short, slender small intestine connects the ventriculus with the sac-like anterior end of the large intestine, to which is also joined a large, thick-walled diverticulum, the intestinal caecum. This caecum is always found, in freshly killed larvae, to be filled with particles of food and countless bacilliform bacteria which are probably symbiotically related to the larva. The large intestine tapers toward the rectum, the junction between these two regions being poorly defined. A comparison of the relatively simple digestive system of a carnivorous tipulid larva such as *Dicranota* (Miall, 1893) with that of moss-eating *Dolichopeza*, with its voluminous divisions and many caeca, recalls similar differences between carnivorous and herbivorous mammals.

Tracheal system.—Two main tracheal trunks extend from the spiracles on the ninth abdominal segment to the anterior part of the mesothorax. They are situated close beneath the dorsolateral body wall, through which they may readily be seen in living larvae. From a bulb-like thickening at the mesothoracic terminus of each trunk, seven branch tracheae are given off to the brain, various parts of the inside of the head, and to the body wall of the prothorax and mesothorax. A metathoracic branch at about mid-length in that segment appears to supply oxygen to the adjacent body wall only. In each abdominal segment from the first through the seventh, there is a pair of ventrolateral tracheal branches, each dividing in turn into a short branch to the muscles and skin of the body wall and a longer visceral branch (Fig. 82); and in each segment there is a slender tracheal connection between the two trunks, passing near the dorsal vessel and probably oxygenating it. Only the bases of these dorsal commissures are indicated in the sketch. The visceral tracheae are longest in the mid-region of the body, where maximum displacement occurs, during locomotion, between the digestive organs and the relatively stationary tracheal trunks. The point of branching from the trunk and the general

visceral destination of the abdominal tracheal branches of one side are summarized as follows:

First abdominal branch: from posterior part of first segment or anterior part of second; to posterior oesophagus and anterior proventriculus.

Second branch: from anterior part of third segment; to proventriculus.

Third branch: from anterior part of fourth segment; to proventriculus and ventriculus in region of caeca.

Fourth branch: from near junction of fourth and fifth segments; to ventriculus.

Fifth branch: from posterior part of fifth segment; to small intestine and posterior part of ventriculus.

Sixth branch: from posterior part of sixth segment; to large intestine.

Seventh branch: from mid-region of seventh segment; to rectum.

The eighth and ninth abdominal segments have no dorsal commissures or visceral branches but are oxygenated by short, much branched tracheae given off just anterior to the spiracle. A few branches from this same source reach the anal lobes, but the tracheation of these is so slight that it seems unlikely that they could serve a respiratory function.

Central nervous system.—As in other crane fly larvae, the brain of *Dolichopeza* is located in the prothorax, outside the head capsule. It is composed of two subspherical lobes, narrowly joined and giving off three anterior branches, which I have not traced but which are presumed to innervate the eyes, antennae and labrum (see Cook, 1949: 39). The brain lies just below and before the open anterior end of the dorsal vessel, or aorta. Circumoesophageal commissures connect the brain with the suboesophageal ganglion, from the anterior surface of which arise two large nerves, each of which divides into three branches innervating certain mouthparts. From the posterior surface of the suboesophageal ganglion, two stout nerve cords converge to connect with the first of a series of four large, rounded and depressed ganglia lying against the floor of the mesothorax and anteriormost metathorax. The first three of these large ganglia supposedly belong to the three thoracic segments, while the last possibly represents the fusion of two or more abdominal ganglia. Ganglia of somewhat smaller size occur in the posterior part of the first abdominal segment, anterior part of the third, near the middle of the fourth, fifth and sixth, and in the anterior half of the seventh abdominal seg-

ments. Some tipulid larvae have one or two additional ganglia, but the equivalents of these in the larva of *Dolichopeza* are unknown. Behind the last ganglion, the two main strands of the ventral nerve cord diverge and bend posterodorsally, giving off several branches. None of the branches of the central nervous system was traced in detail.

Larval key characters.—As stated earlier, most keys to crane fly larvae have made use of characters of the spiracular disc and the head, particularly the mouthparts. Among species of *Dolichopeza,* however, there is such similarity of apperance of the spiracular disc and the lobes surrounding it that I have so far been able to make only limited use of these structures in species recognition; and to utilize details of the head capsule in taxonomy almost always requires dissection of the larva. For life history studies or other reasons, it is often desirable to segregate larvae before preservation. Accordingly, taxonomic characters were sought that would allow species identification of living larvae. A satisfactory means of species separation has been found in the pattern of distribution of the two sizes of microscopic hairs of the integument discussed earlier in this section, used in conjunction with the few reliably consistent differences in the caudal segments.

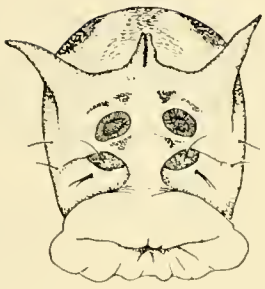
The key that follows has certain limitations. Mature larvae of *Dolichopeza carolus, johnsonella, subvenosa* and two new species described herein are still unknown; and I have reared certain of the other species only a few times and from only a very few localities within their total ranges. The key, however, is reliable to the extent of the material examined. Comments on the species as yet unknown will be found under the respective species headings in the systematic account.

Although prepared on the basis of fourth instar larvae, this key may prove adequate for second and third instar larvae as well. Magnifications of 30 to 80 × have been used in describing characters, but some observations have been verified by use of the compound microscope.

TENTATIVE KEY TO FOURTH INSTAR LARVAE OF NORTH AMERICAN *DOLICHOPEZA*

1. Body coloration in life green with two series of irregular brown to black spots on dorsum (Fig. 97); median lobes above spiracular disc closely appressed; no conical projections from dorsolateral surfaces of eighth abdominal segment (Fig. 91) (subgenus *Dolichopeza*) ..... *americana*

   Body coloration in life greenish, brownish or some blending of these, lacking spots or other markings, except for transverse ridges of small



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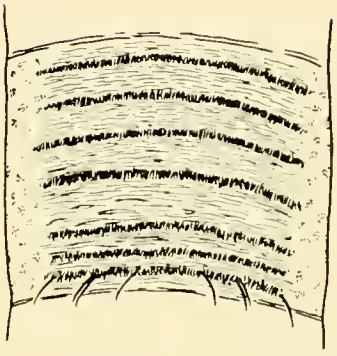

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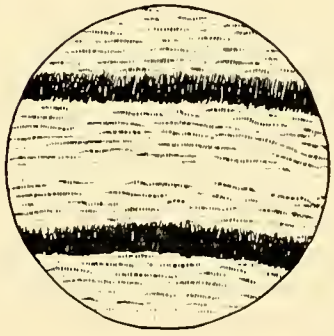

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FIG. 91. Cauda of larva of *Dolichopeza (Dolichopeza) americana*. FIG. 92. Cauda of larva of *Dolichopeza (Oropeza) obscura*. FIG. 93. Typical abdominal segment of fourth instar larva of *Dolichopeza (Oropeza) subalbipes*, dorsal aspect. FIG. 94. Same as 93, *Dolichopeza (Oropeza) obscura*. FIG. 95. Detail of dorsum of fourth instar larva of *Dolichopeza (Oropeza) walleyi*. FIG. 96. Same as 95, *Dolichopeza (Oropeza) sayi*.

hairs; median lobes above spiracular disc distinctly separated; a conical or subconical projection from each dorsolateral surface of eighth abdominal segment (Fig. 92) (subgenus *Oropeza*) 2

2. Minute microscopic hairs of pleura single, thickened and peg-like; those of dorsum sometimes in rows of various lengths but also often occurring singly; transverse ridges of larger microscopic hairs rarely indicated, never dense 3

Minute microscopic hairs of pleura grouped in small, circular patches, the individual hairs not thickened and not seen as separate hairs except at high magnifications; those of dorsum arranged in transverse rows or very rarely single; transverse ridges of larger microscopic hairs evident on most body segments but may be weak on second through sixth abdominal segments 4

3. Minute microscopic hairs of pleura of eighth abdominal segment as numerous, dense or evenly distributed as those of seventh and other segments ..... *polita* sspp.

Minute microscopic hairs of pleura of eighth abdominal segment sparse or irregularly distributed, leaving bare areas ..... *tridenticulata*

4. Larger microscopic hairs of dorsum arranged in dense transverse ridges that are variously interrupted, deflected or staggered (Fig. 93), so that it is difficult to count the number of ridges on a typical abdominal segment 5

Larger microscopic hairs of dorsum arranged in subparallel transverse ridges, usually numbering six or seven per segment (Fig. 94); ridges may be weak on abdominal segments two through six 6

5. Minute microscopic hairs in short rows of varying lengths, the rows distinct, clearly separated ..... *venosa*

Minute microscopic hairs in long, indefinite rows with poorly defined terminations, or not clearly arranged in rows (Fig. 93) .... *subalbipes*

6. Minute microscopic hairs in short, distinct rows with clearly defined terminations, the rows clearly separated (Fig. 95) 7

Minute microscopic hairs in long, indefinite rows with poorly defined terminations, or not clearly arranged in rows (Fig. 96) 8

7. Dorsolateral lobes of eighth abdominal segment nearly conical, of about same shape as lateral lobes above spiracular disc and approximately two-thirds as long as the latter ..... *walleyi*

Dorsolateral lobes of eighth abdominal segment short and blunt, only half or less than half as long as lateral lobes above spiracular disc ..... *similis*

8. Transverse ridges of larger microscopic hairs about equally well marked on all abdominal segments ..... *obscura*

Transverse ridges of larger microscopic hairs more weakly developed on second through fifth (or sixth) abdominal segments than on thoracic, first and seventh abdominal segments 9

9. Minute microscopic hairs clearly in rows, the rows crowded together near transverse ridges of larger microscopic hairs, leaving a narrow zone without hairs (Fig. 96) ..... *sayi*

Minute microscopic hairs usually in poorly defined rows, the rows about evenly distributed between transverse ridges of larger microscopic hairs; hairs long and dense on eighth abdominal segment ..... *dorsalis*

LARVAE—NATURAL HISTORY

It is in the larval state that an individual of *Dolichopeza* passes most of its existence, from only a few days after the egg is laid until about a week before the adult is on the wing. In regions where there are two annual generations, this span of time may be about 280 days in the overwintering generation but only about 50 days in the summer generation (Fig. 99). Larval life comprises four stadia, the last much the longest in duration.

Eggs about to hatch pulsate slightly and irregularly for as much

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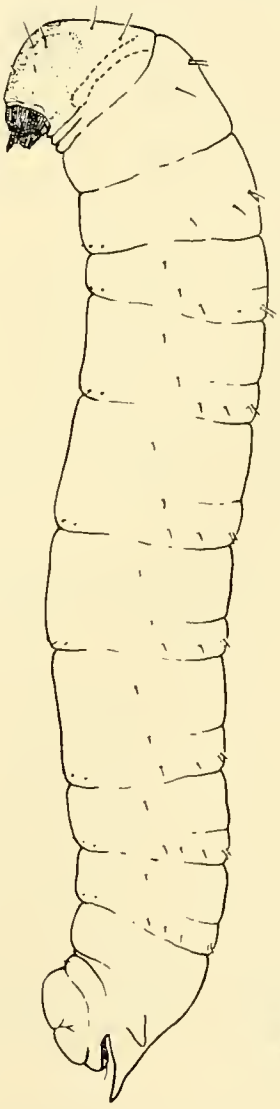

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FIG. 97. Fourth instar larva of *Dolichopeza (Dolichopeza) americana,* dorsal aspect. FIG. 98. Fourth instar larva of *Dolichopeza (Oropeza) obscura* just before emergence of the pupa; note position of head capsule, pupal thoracic respiratory horn visible through larval skin, and contracted lobes of spiracular disc.

as three hours before the chorion ruptures. At hatching, the chorion splits nearly the full length of the egg, mostly along the dorsal side but somewhat on the ventral side, and the head of the young larva appears, mandibles foremost. Grasping at plant fragments or other surrounding objects with its jaws, the larva pulls itself free of the egg covering in a few minutes. Within a few hours the relative proportions of the body of the larva change markedly, as described in the preceding section and illustrated in Figures 78 and 79. Once freed from the egg, the larva sets out almost immediately in search of food, clamping its mandibles firmly into whatever it encounters.* For this reason, newly-hatched larvae in the laboratory must be provided with food, if several are kept together, or they will commence biting each other.

Very young larvae are extremely sensitive to instabilities of environment, such as abrupt changes in temperature or moisture. As mentioned earlier, they drown readily in small excesses of moisture. They perish equally rapidly when subjected to even slight desiccation. Mortality of first instar larvae in the laboratory was very high in all species, possibly because no special equipment was employed to stabilize either humidity or temperature.

Although young larvae appear able by the remarkable gape of their jaws to partake of parts of moss leaves such as are eaten by more mature larvae, their earliest diet seems to consist primarily of material scraped from leaf surfaces and plant scraps which collect about moss stems. Within a day of their emergence, they have gorged themselves so that the alimentary canal may be clearly seen as a bright green streak from one end to the other of the nearly transparent body. Confined to small dishes in the laboratory, very young larvae frequently devoured others that had died, and somehow opened and consumed the contents of unhatched, presumably unfertilized eggs, discarding the chorion. I do not take it from this that cannibalism is the rule in *Dolichopeza* but merely assume that available sources of protein are utilized whenever they are found by young larvae, just as they are by older larvae, which have been observed to feed on dead pupae and larvae in laboratory rearing dishes.

Duration of the first stadium is not constant, even among larvae of the same brood hatched about the same time. It usually varied from eight to fifteen days, indoors, although a few laggard individ-

* This tactile response of the mandibles is a convenience in picking up the tiny larvae, which might be damaged by other means. A hair or bristle of a brush placed before the larva is soon seized between the jaws, and in the time it takes the larva to discover it has not got hold of food, it may be transferred to the desired place.

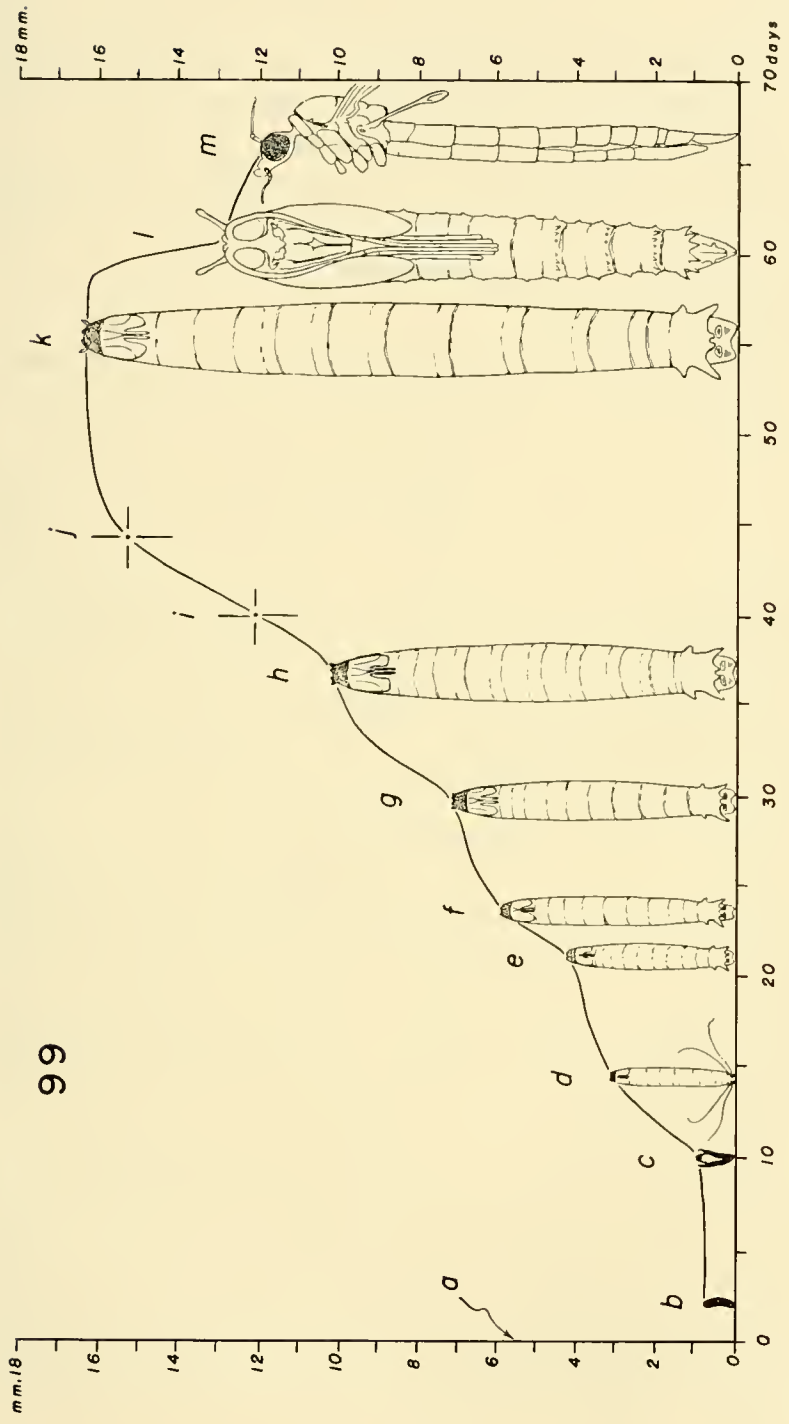


FIG. 99. Life cycle and growth in the summer generation of *Dolichopeza (Oropeza) sayi* in southern Michigan; a—time of oviposition, b—egg, c—hatching of egg, d—first instar larva, e-f—second instar larva, g—third instar larva, h—early fourth instar larva, i-j—growth indicators, fourth instar larva, k—late fourth instar larva, l—pupa, m—adult female.

uals required three weeks to pass to the next instar. Larvae reach a length of about four millimeters before the first ecdysis. Size change at molting is not noticeable, but some remarkable changes take place in the appearance of the larva. The four long caudal setae as well as the tufts of bristles (Fig. 81) are shed with the first larval skin. These structures are characteristic of the first instar larva of all species in which this instar was observed (*americana, carolus, dorsalis, johnsonella, obscura, polita* sspp., *sayi, similis, venosa* and *walleyi*); accordingly, their absence is taken as evidence that the first molt has occurred.

In the second instar, the larva of *Dolichopeza* resembles the later instars in general appearance. Although low and broad, the characteristic six lobes surrounding the spiracular disc are present and plainly visible, as are also the dorsolateral lobes of the eighth abdominal segment. At the first molt the larva also acquires the coating of microscopic hairs that gives the body the roughened surface so useful in locomotion. (There are hairs on the skin of the first instar larva, but they are so short and slender as to be scarcely visible at 200 × magnification.) Following the first ecdysis, the larva feeds more actively and grows rapidly, reaching the end of the second stadium in about five or six days.

Third and fourth instar larvae are almost identical in appearance, differing only in size. The third stadium may be as short as five days, so that some larvae may attain the fourth instar only about three weeks after hatching from the egg. Thus, the fourth stadium lasts as long as the other three combined, in the summer generation, and is much longer in the overwintering generation. Size increase is especially rapid during the first few days following a molt, in all instars (Fig. 99), and thereafter it proceeds more slowly. An explanation for this may be found in the fact that the larva ceases to eat for a short time preceding ecdysis, but once the mouthparts regain their strength and rigidity after the molt it commences to eat voraciously. Of those larvae that survived, in a rearing dish of *Dolichopeza sayi,* all that hatched on or about 26 September reached the fourth instar between 15 October and 5 November, indoors. This was in southern Michigan, where sunny days are common enough into late October that most larvae produced from late summer matings are able to attain the fourth, or at least the late third, instar before cold weather forces cessation of feeding and the winter quiescence.

Molting.—Several hours before shedding its skin, the larva of *Dolichopeza* ceases feeding and other activities, and the body slowly becomes turgid, assuming a swollen appearance like that sometimes seen in larvae that have been dead several hours. The caudal lobes become tumid and blunt, losing their nearly-conical shape, and the spiracular disc bulges outward. The head is fully extended, while the thorax close behind it is swollen with the skin darkened, almost black. In this inactive condition, the larva rests until the separation of old cuticle from new has been completed. When movement is resumed, shortly before the actual molt begins, a perfect duplication of bristles, microscopic hairs and all other external features of the larva may be seen through the old integument. The larva suddenly begins to jerk the anterior one-third or one-half of its body from side to side in frantic and spasmodic motions, the head capsule being bent further and further ventrad all the while. About two minutes after the onset of this activity, the skin splits along the dorsal mid-line of the thorax, just behind the old head capsule, and the head of the larva is thrust out. Only another sixty seconds or so are required for the virtual completion of sloughing off the old skin, as the pale and feeble larva crawls among the moss stems, working the old skin off by repeated body undulations and by scraping against its surroundings. Attached at the spiracular disc by the linings of the tracheal trunks, the crumpled molted skin is dragged about for a while and is nearly turned inside out before the tracheal linings pull out and the larva is at last free of its old skin. Each ecdysis seems to produce a double crisis in the life of the larva, first in the struggle to throw off the old skin and second in surviving the periods of comparative helplessness before and after the molt. In fact, I find it somewhat fatiguing merely to observe the process!

Each of the four larval instars of a given species may be recognized by the dimensions of the head capsule, which changes size abruptly at molting while the softer parts of the body increase gradually and continuously. Increase in breadth of the larval head by a more or less fixed factor at each ecdysis has been observed in many kinds of insects and has been summarized as Dyar's law. In *Dolichopeza (O.) sayi*, this fixed factor of increase was found to be 1.5. Thus, from the head capsule width of the first instar larva measured as 0.25 mm., one estimates 0.38 mm. as the width of the second, 0.57 mm. for the third, and 0.86 mm. for the fourth instar head capsule. Observed widths were 0.25 mm., 0.40

mm., 0.60 mm. and 0.85 mm., respectively, measured by means of a camera lucida scale. Head capsule length in this same series of specimens averaged 0.40 mm., 0.65 mm., 1.00 mm. and 1.50 mm. for the four larval instars, showing that length increase is not exactly proportional to width increase. In a single instance, a larva seemed, on the basis of the size of head capsule recovered from the pupal burrow, to have pupated at the end of the third stadium. No indication of a fifth instar was ever found.

Feeding.—Very young *Dolichopeza* larvae are able to obtain food by scraping the surfaces of moss leaves and may also eat organic debris of various sorts, including their own dead. From the fact that often only the head capsule could be recovered from a rearing dish soon after a larva had molted and that I once found a larva with its head directed toward its freshly-cast skin, I suspect that the larva may often eat its recent skin for its first meal following ecdysis. By far the greatest item in the diet of the second, third and fourth instar larvae, however, is leaves of certain mosses and leafy liverworts. The particular species of such food plants are listed later in this section, under ecological distribution.

Most feeding is done at or near the surface of the moss habitat, where the leaves are green and fresh. When isolated bits of moss are offered to larvae in rearing dishes, the leaves are largely or entirely consumed, while the stems and other parts are ordinarily rejected.

There is an interesting difference in feeding behavior between larvae of *Dolichopeza americana* and those of species of subgenus *Oropeza*. Larvae of all species of *Oropeza* are rather uniformly colored, brownish, greenish or some subtle blending of these (the color in any case largely dependent upon recent diet) and in general lack any pattern. Transverse ridges of microscopic hairs might be regarded as a pattern, but this is not of the obliterative sort that draws attention away from the shape of the insect. Therefore, *Oropeza* larvae are conspicuous against the background of greenish highlights and dark shadows characteristic of most mossy surfaces on which they feed. *Dolichopeza americana,* on the other hand, has a green color and is irregularly marked with dark lines and blotches (Fig. 97) which serve remarkably well to break up the visual outline of the insect. And while larvae of *Oropeza* conceal themselves well down in the moss by day and feed almost wholly at night, *americana* often browses at the surface in full daylight. Larvae of *americana* may also be found more deeply in the moss by day, but it is a rare occurrence to find an *Oropeza* larva exposed

to view.* Occasionally the irregularly-shaped, green and brown larvae of *Liogma nodicornis* (Tipulidae: Cylindrotiminae) are found on the same moss with *Dolichopeza americana*, and a similarly-colored and patterned moth caterpillar (Noctuidae—my identification) was three times taken together with these two species of tipulid larvae, all providing striking examples of protective resemblance of insect to environment. It seems clear to me that there is a correlation of color pattern in *Dolichopeza* larvae with the time of active feeding.

Locomotion.—In the field the collector will probably find larvae of *Dolichopeza* in an inactive state in which the anal lobes are withdrawn and the head is retracted within the second and/or third thoracic segments. This is the attitude assumed by the larva in reaction to tactile or light stimuli, as it shrinks from both. In this position, the larva may remain quite motionless for many minutes. When the irritation has eased or ceased, the larva puts out its head, protrudes the anal lobes and proceeds to a place of concealment. Lacking any sort of creeping welts such as are found on larvae of some other genera of Tipulidae, the larva of *Dolichopeza* accomplishes locomotion by three other means. It may move slowly by extension and contraction of the body, using the rough skin and large bristles as braces against the surrounding medium. More rapid locomotion is achieved by the pushing action of the anal lobes in combination with bodily undulations. Sometimes the head is extended forward and a moss stem or other support is grasped between the mandibles, so that the body may be pulled forward by contraction. This method of getting around is occasionally used alone but more often simultaneously with one or both other means described.

Preparation for pupation.—Larvae not feeding at the moss surface will ordinarily be found just beneath the surface in fairly well formed tubes. Close examination of such a tube shows that it is constructed not by the larva's having eaten or forced its way through firm material or dense moss but rather by caulking larger, pre-existing cracks with a frass of digested moss fragments and other debris. Larvae do not penetrate more than a few millimeters into wood or soil upon which their moss habitat occurs, and they have never been found in any but the most spongy, soft wood in advanced stages of decay. A tube thus formed is of course usually

* To collect larvae from mosses brought into the laboratory, I have spread the mosses in a pan, leafy surface upward, and covered them with a few sheets of dampened newspaper. After a few hours in this artificial darkness, larvae may be found feeding at the surface of the moss.

closed behind the larva and is shifted from place to place according to available food and appropriate sites. But in the last days of its fourth stadium, the larva prepares a more compactly walled tube, oriented roughly parallel to the moss surface and with an open anterior end curving up to the surface. It is within this tube that pupation occurs and the pupal stage is spent. The pupal burrow is usually about one and a half times as long as the pupa but has been found as short as one and a quarter times the length of the pupa in *Dolichopeza subalbipes* and as long as twice the pupal length in *venosa*.

Pupation.—As the pupa takes shape within the skin of the fourth instar larva, the larval head capsule is pushed slowly forward and downward. In an individual about to undergo the transformation from larva to pupa (that is, the actual molt), the pupal structures become visible through the larval cuticle only a few hours before ecdysis. The head capsule becomes sharply deflected downward, about two hours prior to the molt, until its longitudinal axis forms an acute angle with that of the body generally (Fig. 98), stretching the skin of the prothoracic dorsum taut. The lobes surrounding the spiracular disc are drawn together in such a way as nearly to conceal the spiracles. A period of about fifteen minutes of relative inactivity was noted to precede the molt, following which occurred an abrupt resumption of movement, terminating after only a few minutes in the splitting of the old head capsule and prothoracic skin and the rapid emergence of the pupa. Worked off backwards by bodily undulations of the pupa, the old larval skin is pushed into the back of the burrow, in the form of a small, blackish, wrinkled wad, scarcely recognizable from surrounding frass and other debris, except for the head capsule. With some knowledge of the usual length of the pupal burrow, one ordinarily may recover the shed last larval skin rather easily by watching for the head capsule. If the skin is not recovered and preserved within a couple of days after pupation, however, decomposition sets in, and various organisms, chiefly mites and Collembola, begin to feed on it, destroying all but the strongly sclerotized head.

Seasonal distribution.—It has been my repeated observation that not only is the late summer generation of adults composed of individuals smaller than those of the spring generation, for reasons presented earlier, but also that there are fewer flies in the late summer generation. Several explanations for this are possible, such as the likelihood of a greater amount of parasitism or predation on larvae

during the summer, or starvation or desiccation of larvae due to summer drouth conditions. It seems not improbable, however, that it may be due, at least in part, to differential rates of larval development; that is to say, some larvae in favorable habitats complete all their growth stadia, pupate and produce the fall generation adults, while others in more marginal habitats possibly attain the fourth larval instar but are prevented from growing rapidly enough to pupate in late summer and as a result overwinter as larvae. The result of this would be a spring generation of adults derived from larvae some of which are approximately nine months old and others of which are nearly a year old. Intensive field observation of larvae at a particular locality through an entire year would probably provide an answer to this problem.

The seasons for collecting larvae in various instars have been discussed under the heading of collection and preparation of material for study.

Exploration of larval habitats during the spring, summer and autumn shows that the larvae seldom penetrate more than a few millimeters, perhaps a centimeter, below the surface of their bryophyte food supplies and then only into soft substrata such as rotten wood or soil. I was curious to know where they spent the winter, whether still near the surface or deep beneath the moss, burrowing downward like the immature stages of some other kinds of insects. Plainly, those larvae that lived in the shallow growth of moss covering boulders or rock cliffs could not go very far from the surface to escape winter's cold. And there are not many places in the northern parts of the range of the genus where larvae could go below the frost line. In order to answer this question, I marked several microenvironments (that is, particular patches or hummocks of moss) found to contain numerous larvae in late summer and fall and revisited these in midwinter. While some of the larvae had gone a short distance below the surface, most were in about the same places where they had been active during warmer weather. From moss solidly frozen in a cake of ice that was chopped from the floor of a marsh in Michigan on 31 December, I succeeded in rearing *Dolichopeza sayi.* A larva thawed from the ice slowly extended its contracted body as it warmed in the laboratory, and after a few hours it was actively feeding. By 30 January, this larva had developed into an adult fly.

By remaining at or near the surface, larvae are able to take advantage of occasional warm days, in late autumn and early spring, to feed. Furthermore, drainage of the microenvironment is suffi-

cient in most instances to protect the larvae from becoming frozen within a formation of ice; but even if so frozen, they are able, at least some of the time, to survive. Physiological adaptations, such as supercooling, reduction of body water with consequently higher salt concentration in the haemolymph, adsorption of water on protein molecules, an so on, surely enable the larvae to withstand many of the low temperatures to which they are subjected. It is not inconceivable that in their contracted state they are able to conserve at least for a while minute amounts of radiant heat received at times when there is no snow cover. In spite of all this, I believe winter weather does take an appreciable toll, for the spring populations of larvae are much reduced from those of the autumn, and there is not likely to have been extensive predation in winter.

Ecological distribution.—It is possible to describe the general habitats of the various species of *Dolichopeza* in rather broad terms, such as swamps and marshes, rocky ravines, mesic woodlands, and the like; but what is actually described in these cases is the kind of place in which adults of the species may be found. These habitats, for the various species and species groups of *Dolichopeza,* have already been discussed under the natural history of adults. Within or adjacent to these broad and not always well-defined types of habitats, the microhabitats of the larvae may be widely distributed or narrowly restricted.

Larval microhabitats have been discovered for all North American species of *Dolichopeza,* except the two new species described herein, and in all cases the food substance was a moss or liverwort, although larvae may occasionally be found in the various substrata upon which the bryophyte is growing (cf. Alexander, 1920: 981). Larvae of most species of *Dolichopeza* have been observed to feed on a variety of bryophytes, a variety that will surely be found vastly increased as observations are continued. It might therefore appear that the distribution of a particular species is controlled by the distribution of the bryophytes upon which its larvae can subsist. This, however, is only partly true. Whatever mosses or liverworts are utilized by *Dolichopeza* as larval habitats are those the microenvironmental characteristics of which are to a large measure conditioned by the general environment in which they are growing. While it is true that most bryophytes have fairly limited ranges of ecological tolerance, some grow under various conditions. Therefore, it does not follow that, if larvae of a species of *Dolichopeza* have been found feeding on a particular kind of moss, wherever that moss occurs there will be found also the fly. For ex-

ample, *Leucobryum glaucum* growing loosely and luxuriantly on hummocks in a birch-maple swamp is a known, albeit uncommon, larval habitat for *Dolichopeza obscura;* but I would not expect to find *obscura* larvae in that same species of moss growing, as it does much more often, in compact, dry cushions on the floor of a hilltop oak-hickory woods. *Hedwigia albicans*, growing usually on exposed rocks, is a dry, blackish moss that seems an unlikely habitat for any crane fly larva. But if the rocks were in a wooded area, shaded by trees, the moss could retain enough moisture to support larvae of *Dolichopeza tridenticulata*, a species much more tolerant of dry conditions than any other in the genus (see Alexander, 1920: 983, under *Oropeza obscura*).

That it is the conditioning effect of the general environment on the microhabitat and not the general environment itself that governs the distribution of larvae of *Dolichopeza* is shown by the fact that where appropriate microhabitats obtain in contrasting kinds of general environments the crane flies may be found. *Dolichopeza sayi*, for example, seems to find the ecological conditions required by its immature stages rather generally available along the shaded borders of northern swamps and marshes, and its larvae are found widely scattered there in the mosses of the swamp floor and hummocks. By contrast, in an area of rocky ravines, where *sayi* is present in much smaller numbers and where adults were seen only in a limited area of vegetation in the bottom of a ravine, larvae were found only around one small patch of swampy soil, only a few square feet in extent, below a permanent seepage from the cliff. It is thus not the swamp type of general environment that limits the distribution of the species. As a further example, larvae of *Dolichopeza tridenticulata* occur in great numbers in thin growths of moss on boulders and rocky walls of gorges in southern Indiana and Ohio, but the species also finds a vastly more limited yet somehow satisfactory habitat in a sparse growth of moss in crevices of tree bark in a woodland on comparatively level ground, in southern Michigan.

Precisely what the larvae need from their surroundings has not been studied in detail. Their reactions in the laboratory to excess moisture and to desiccation have supplied some information, however, about their ecological requirements. Very young larvae are easily drowned in even a small amount of water, when they are unable to extricate themselves from it. If its moss habitat becomes flooded, a larva in an advanced stage of development first closes together the upper and lower lobes of its spiracular disc, then ex-

tends its caudal end up to the surface, exposing the spiracles to the open air. The surface of the disc is very smooth and apparently repels water, while the lobes surrounding it so effectively hold back the surface film of the water that the disc may actually be withdrawn very slightly below the surrounding water level without being wetted. A submerged larva also extends its head, making the body fully outstretched.* If the water does not soon recede, the larva begins to crawl toward a drier place, periodically pausing and putting its spiracles to the surface for air.

If a larva is removed from damp moss and placed in an empty dish or on a tabletop, it will wander about aimlessly until the cuticle dries. At this point, the larva retracts its head and anal lobes, decreases the exposure of its spiracular disc by drawing the lobes closer together, and contracts its entire body, thus reducing the evaporation surface. Movement ceases, and unless restored to a moist environment the larva will continue to lose body fluids through the skin and will shrivel and die on that spot.

In view of these reactions to drying and excessive wetting, one may make some generalizations about the bryophyte habitats of larvae of *Dolichopeza*. It seems unlikely, for example, that primarily aquatic mosses, such as *Fontinalis* or some species of *Drepanocladus* or *Hygrohypnum* would be utilized. The same could be said of mosses that ordinarily grow in dry places, such as *Grimmia*, *Ceratodon* and *Hedwigia*, although it has been shown that such mosses may, when their usual ecological situation is modified, support these larvae. It of course follows from this that whatever bryophytes are utilized must not at any time during the larval part of the crane fly life cycle become inundated or desiccated for a prolonged period, if the larvae are to survive. On the other hand, it seems not unlikely that larvae do perish as a result of oviposition in such fluctuating, marginal microhabitats that happened to have been in a favorable condition during the season for oviposition.

Larvae of *Dolichopeza* were sought in all kinds of mosses and liverworts available, as well as in soil, decayed wood, fungi and other plants, leaf litter, and the like. They were found in a wide variety of bryophytes, which demonstrates a certain latitude in their ecological tolerance, but some generalizations about their habitat preferences may be gained also, I believe, from the bryophytes in which they were not found. Aside from never having been found in aquatic or in very dry mosses, as discussed above, they were never collected either from loosely-growing, bushy mosses

* This initial reaction to inundation is useful in obtaining over-all measurements of living larvae.

or from those that grow in tightly-arranged tufts or patches. I suspect that the very compactly-growing mosses, such as *Bryum argenteum* or *Ceratodon purpureus,* even if growing in the appropriate environment, would offer too much resistance to the tunneling larvae, while the loosely-growing mosses, such as *Climacium, Rhodobryum, Polytrichum* and most *Mnium cuspidatum,* present too diffuse a framework for the construction of burrows by the caulking method described earlier.

Not only the growth habit of the bryophyte but also its leaf texture affects the crane fly's selection of microhabitat, or at least its choice of food. Coarse-leaved mosses like *Polytrichum* were always rejected, when offered to larvae in laboratory rearing dishes, and apparently are not eaten under natural conditions. Bryophytes with thick leaves, such as the thallose liverworts, seem not to be eaten either. In a mixed growth of leafy *Mnium punctatum* moss and the thallose liverwort, *Pellia epiphylla,* larvae of *Dolichopeza americana* fed exclusively, as far as could be determined by field observation, on the *Mnium.*

It scarcely need be mentioned that mosses which do not occur anywhere about the various general environments of *Dolichopeza* are not likely larval habitats. These would include some moss species that usually grow on sand or clay in open fields, in seashore habitats, and other unforested places. Many such mosses were collected and examined, however, during the early stages of this investigation.

Where several species of *Dolichopeza* occur within one general environment, as is usually the case, each species has its characteristic larval microhabitat, although these often overlap broadly, resulting at times in the occupation of a single clump of moss by larvae of as many as three species. In a swarm of adults under a rock ledge in a wooded ravine, I may find together adults of *Dolichopeza obscura, tridenticulata, polita, walleyi* and *americana.* A search for the immature stages might show, however, that *obscura* came from *Hypnum* moss growing on a rotten log, *tridenticulata* from *Dicranella* on the rather dry upper surface of a large boulder, *polita* from mixed *Tetraphis* moss and powdery lichen on the moist undercut surface of the rock outcrop, *walleyi* from *Plagiothecium* growing as a mat on the rich soil of the floor of the ravine, and *americana* from *Mnium* growing on the damp rock at the base of the cliff.

More than fifty species of bryophytes have been found associated

with larvae of *Dolichopeza*, ranging from rather dry *Dicranella* on boulders to decidedly wet *Amblystegium* of swamps, from calcareous, marl-forming *Gymnostomum* to acidic *Sphagnum*, and from fairly compact cushions of *Tetraphis* to the loose mats of certain liverworts or the low, leafy clumps of *Mnium*. In general, these microhabitat plants are those through which the larvae can move freely but which are at the same time compact enough to permit burrow formation * and which are not excluded for any of the reasons stated above.

Certain species of *Dolichopeza* have so far been found usually in mosses that were only damp, while other species have always been collected from wet mosses. A correlation between species of crane fly and the amount of moisture in its larval habitat can be indicated by a rather arbitrary arrangement set forth in Table 3. In this table, known food plants are arranged from the driest at the top to the wettest at the bottom. As many mosses will grow under diverse conditions, they are entered in the table according to their relative water content at the time of collection. The species of *Dolichopeza* are arranged from left to right across the top of the table in the order which I believe expresses their increasing affinity for moisture. Mosses in particular but liverworts as well are often found growing in close associations of two or more species. The following mosses and liverwort were collected together with food plants listed in the table and are possible or probable food sources for the larvae, although the relationship has not been established: *Anomodon attenuatus, Anomodon rostratus, Aulacomnium palustre, Brachythecium* sp., *Dicranella* sp., *Dicranum flagellare, Drepanocladus aduncus, Lophcolea heterophylla, Mnium cuspidatum, Thuidium delicatulum* and *Thuidium recognitum*.

Although several larval microhabitats have been discovered, there must be a great many more still unknown. When I compare, in the field, the number of adults on the wing with the number of pupal skins found (or the number of larvae that could have been found at an earlier date), it sometimes seems to me that I have scarcely touched upon their major moss habitats, that I might have overlooked the most important places. This of course is largely a result of the diffuse distribution of the immature stages and the concentration of adults in places not always near the larval habitats.

* So often do the larvae follow lines of least resistance in moving through moss that a convenient way to collect them from fairly compact cushions is to bend the leafy outer surface of the moss into a convex curve until it opens along naturally formed cracks. In these cracks will be found nearly all the larvae which inhabit the particular bit of moss.

A systematic arrangement, by family, of the habitat bryophytes listed in Table 3 illustrates something of the range of plants of this phylum that are utilized by larvae of *Dolichopeza*. Eleven of the twenty-seven families of mosses known from North America are represented, and of those not appearing here many are specialized families including only a few species. The family Hypnaceae, by far the largest in this continent, is not disproportionately represented by the sixteen listed species. In contrast to the broad distribution of food plants among the mosses, all five species of liverworts fall into a single family, the Jungermanniaceae, or leafy liverworts, which are not unlike mosses in leaf texture. The other five families are so far unknown as *Dolichopeza* habitats, and it seems that most of the liverwort habitats yet to be discovered will also be species of the Jungermanniaceae.

MOSSES

Sphagnaceae: *Sphagnum palustre, Sphagnum* sp.
Georgiaceae: *Tetraphis pellucida*
Polytrichaceae: *Atrichum macmillani, Atrichum undulatum*
Fissidentaceae: *Fissidens taxifolius*
Dicranaceae: *Dicranella heteromalla, Dicranum scoparium, Leucobryum glaucum*
Grimmiaceae: *Hedwigia albicans*
Tortulaceae: *Desmatodon obtusifolius, Didymodon tophaceus, Gymnostomum calcareum*
Orthotrichaceae: *Orthotrichum sordidum*
Bryaceae: *Leptobryum pyriforme, Mnium affine, Mnium punctatum, Mnium* sp.
Leskeaceae: *Myurella careyana*
Hypnaceae: *Amblystegium riparium, Amblystegium varium, Brachythecium salebrosum, Bryhnia graminicolor, Campylium chrysophyllum, Entodon cladorrhizans, Eurhynchium pulchellum, Eurhynchium serrulatum, Heterophyllium haldanianum, Hypum curvifolium, Hypnum imponens, Hypnum lindbergii, Hypnum* sp., *Plagiothecium denticulatum, Plagiothecium deplanatum, Plagiothecium roeseanum, Platygyrium repens.*

LIVERWORTS

Jungermanniaceae: *Calypogeia trichomanis, Chiloscyphus pallescens, Geocalyx graveolens, Plagiochila asplenioides, Scapania nemorosa.*

In examining bryophytes for the larvae of *Dolichopeza*, one repeatedly comes across certain other organisms, mostly arthropods but, if the plants are from wet habitats, molluscs as well. Those most regularly found in association with *Dolichopeza* larvae are small pyralidoid caterpillars (identified by Mr. H. W. Capps), various stratiomyid larvae (unidentified, occurring in wet mosses especially), several species of Collembola (Entomobryidae, Po-

TABLE 3.—Distribution of Larvae of Species of North American *Dolichopeza* in Bryophyte Microhabitats Arranged According to Moisture Content

BRYOPHYTE HABITAT	Species of *Dolichopeza*												
	trident'ata	polita	americana	venosa	obscura	johnsonella	subvenosa	walleyi	subalbipes	carolus	similis	sayi	dorsalis
Hedwigia albicans, on rocks	×												
Dicranella heteromalla, on upper surface of boulder in woods	×												
Orthotrichum sordidum, in crevices of tree bark, in woods	×												
Tetraphis pellucida, with powdery lichen, shaded sandstone cliff	×	×	×										
Calypogeia trichomanis, on shaded sandstone cliff		×											
Atrichum macmillani, on sandstone cliff		×	×										
Leucobryum glaucum, near base of sandstone cliff in woods		×	×										
Dicranella heteromalla, near base of sandstone cliff		×	×										
Bryhnia graminicolor, on exposed clay bank			×										
Plagiothecium roeseanum, on trapped soil, sandstone cliff		×		×									
Hypnum sp., on trapped soil, sandstone cliff		×											

Platygerium repens, on bark of fallen tree, in hardwoods								×					
Myurella careyana, on sandstone cliff		×											
Plagiochila asplenioides, on sandstone cliff		×	×										
Eurhynchium serrulatum, on trapped soil, sandstone cliff		×											
Scapania nemorosa, on sandstone talus rock		×											
Mnium punctatum, at base of damp sandstone cliff		×	×										
Atrichum undulatum, on glacial till slope								×					
Chiloscyphus pallescens, on glacial till slope					×								
Leptobryum pyriforme, at base of wet sandstone cliff				×									
Mnium sp., on damp soil, bank of brook, in woods							×						
Campylium chrysophyllum, on wet sandstone cliff		×											
Desmatodon obtusifolius, on wet sandstone cliff		×											
Tetraphis pellucida, on swamp hummocks					×				×		×		
Geocalyx graveolens, on swamp hummocks									×				
Plagiothecium deplanatum, on stream bank in woods								×					
Entodon cladorrhizans, on clay soil, stream bank								×					
Leucobryum glaucum, on bank beside spring			×							×			

TABLE 3.—Distribution of Larvae of Species of North American *Dolichopeza* in Bryophyte Microhabitats Arranged According to Moisture Content—*Concluded*

BRYOPHYTE HABITAT	Species of *Dolichopeza*													
	trident'ata	polita	americana	venosa	obscura	johnsonella	subvenosa	walleyi	subalbipes	carolus	similis	sayi	dorsalis
Tetraphis pellucida, on bank beside spring			×							×			
Hypnum imponens, on soil beside stream, in woods			×					×					
Dicranum scoparium, on hummocks in swamp									×		×		
Hypnum curvifolium, on hummocks in swamp					×								
Leucobryum glaucum, on hummocks in swamp					×								
Heterophyllium haldanianum, on rotten wood, in swamp					×						×	×	
Plagiothecium denticulatum, on tree bases, in swamp											×		
Fissidens taxifolius, on boggy, shaded soil					×								
Gymnostomum calcareum, in seepage over sandstone		×				×							
Amblystegium riparium, at margin of woods pool								×					

Mnium affine, at margin of woods pool								×					
Didymodon tophaceus, on sandstone, at waterline												×	
Eurhynchium pulchellum, at margin of swamp, on soil												×	
Brachythecium salebrosum, swamp margin, on soil												×	
Hypnum lindbergii, on wet soil at edge of swamp												×	
Sphagnum palustre, wooded zone of bog													×
Sphagnum sp., bog, at edge of tree zone													×
Amblystegium varium, on floor of marsh												×	×

duridae and Sminthuridae), and numerous species of Acarina, notably the "beetle mites" (Oribatoidea) and parasitoid mites. Of these, the lepidopterous larvae are worthy of further comment, here, for their trails through the mosses may often be mistaken for those of *Dolichopeza*. These caterpillars usually had reached a length of about 5 to 8 mm. by the time I first noticed them, and I saw some over a centimeter long, which I took to be later instars. The caterpillars are of a reddish brown color, sparsely haired, with large, glossy brown heads. They are extremely active creatures and ravenous eaters of moss. Their tunnels in the moss are frequently lined with webby silk fibers and are always littered with fecal pellets, which is what makes them resemble the trails of *Dolichopeza*. I feel fairly certain that these common pyralidoid caterpillars are the immatures of small, light brown or light grayish moths that are often taken in the rearing dishes. Mr. Sherman Moore, of Detroit, has identified several of the moths as *Crambus alboclevellus* Zell. (from *Mnium cuspidatum*), *C. elegans* Clem. (from *Aulacomnium palustre*), *C. albellus* Clem. (from *Amblystegium varium*), and *Crambus* sp. (from *Dicranum scoparium*).

Mosses and liverworts while harboring many kinds of organisms appear to furnish food directly to only a few, such as the moth larvae just mentioned and certain kinds of Tipulidae. From the rock gorge habitats, I have reared *Tipula* (*Oreomyza*) *ignobilis, Tipula* (*O.*) *fragilis, Liogma nodicornis, Limonia* (*Dicranomyia*) sp., *Erioptera* (*Symplecta*) *cana* and *Gonomyia* sp. From mosses of northern marsh borders, *Tipula* (*Yamatotipula*) *sulphurea, Tipula* (*Trichotipula*) *oropezoides* and *Limonia* (*Dicranomyia*) *immodesta* were reared, together with *Dolichopeza sayi*.

In a discussion of the ecological relationships of the larvae of *Dolichopeza*, it seems appropriate to mention associations of larvae of various species within the genus, for it often happens that the larvae, like the adults, keep close company. Within an area of *Tetraphis* moss no more than three inches in diameter, for example, may be found larvae of *americana, polita* and *tridenticulata*. Larvae of *obscura* and *subalbipes* often occur together in the mosses of swamp hummocks. Other such associations are suggested in Table 3. The important thing about these close interspecies associations is that there appears to be no competition whatsoever. There seems to be always enough moss to feed all the larvae and to keep them comfortably apart from one another. Rarely does a natural growth of moss contain so many larvae that noticeable defoliation results; in fact, I have observed only one such occurrence,

in which several larvae of *Dolichopeza americana* and *Liogma nodicornis* feeding on a thin growth of *Mnium punctatum* on a sandstone cliff had conspicuously damaged an area perhaps four inches in diameter. If larvae do encounter each other occasionally during their tunneling, it seems unlikely that competition in the form of fighting would result. Even when several larvae are confined in a dish without moss, they do not show any aggressive behavior (such as is known among some other tipuline larvae) and could be described in general as lethargic. In view of these facts, it is difficult to imagine what form interspecies competition among larvae might take.

Parasites and predators.—Probably the most important difficulties with which the life of the larva is beset, except for the rigors of weather already mentioned, are predation and disease (including parasitism). There would be no point to enumerating those organisms that might prey on *Dolichopeza* larvae. The survey of predators on the Tipulidae in general given by Alexander (1920:721 ff.) will suggest several possible ones. The only time I have actually witnessed predation on a *Dolichopeza* larva was an instance of *D. walleyi* attacked by a larva of a small species of *Tabanus* * in the moss *Hypnum imponens* growing at the edge of a woodland pool in southern Michigan.

Evidence of parasitism is as rare as that of predation, and there are no established records of parasites in or on the larvae of *Dolichopeza.* Certain hymenopterous parasites that become evident only during the pupal stage of the crane fly host (see section on pupal life history) must occur within the larva throughout its life but do not hinder its activities and allow it to grow and metamorphose. In rearing dishes I have found the braconid wasp, *Macrocentrus reticulatus Muesebeck,* and an ichneumonid, *Mesoleptus* sp. † Concerning these, Dr. Muesebeck wrote: "The *Macrocentrus* must be a parasite of some lepidopterous larvae although no host seems yet to have been recorded for *M. reticulatus.* For species of *Mesoleptus* we have little host information. There are some records of the rearing of specimens of this genus from Diptera but I do not know how authentic these are."

Parasitism in certain crane flies other than *Dolichopeza,* which were observed, may be relevant here, inasmuch as the larvae involved were taken in microhabitats of *Dolichopeza.* Perhaps the

* Identified by Dr. W. W. Wirth, U. S. National Museum.

† Dr. Muesebeck identified the braconid, which was the first male of the species to come to his attention. Miss L. M. Walkley determined the ichneumonid.

most spectacular case was that of a nematode infestation of a larva of *Tipula,* found in a moribund condition. Two large, whitish nematodes, one nearly 20 mm. long and the other over 30 mm. in length, were subsequently found to have pierced the body wall of their 16 mm. host and just completed their escape. Postmortem examination of the larva showed the internal organs to be intact but the usual sheet of fat absent. The skin around the two exit holes was thickened and blackish, and the larva was left quite limp and somewhat flattened. This is the first instance of nematode infestation of a crane fly larva to come to my attention, although it must be a common occurrence in nature.

A bacterial infection causing eversion of a portion of the caudal end of the digestive tube has been observed in three species of tipuline larvae. Internal symptoms include nodular growths on all major portions of the alimentary canal. From these whitish cysts, smears were prepared. The contents were found to consist of many small, fat-like globules and highly motile, short rod bacilli, which proved to be gram negative. Colonies of the bacilli on blood agar were gray-buff in color, with a definitely cleared zone eight millimeters in width surrounding them. While this disease kills larvae within two days of appearance of first symptoms, I was not successful in inoculating larvae of *Dolichopeza* with the bacilli.

PUPAE—MORPHOLOGY

Size of the pupa depends upon both species and environment and is directly proportional to and smaller than the size of the fourth instar larva, just before pupation (Fig. 99). Pupae of the smaller species (*americana, dorsalis* and *tridenticulata*) are commonly only 10 or 11 mm. long, while those of larger species (such as *similis*) reach lengths of 16 mm. or more. Measurement of both whole pupae and cast pupal skins is subject to the same sort of error as occurs in measurement of the other life history stages, due to the position of the insect—whether outstretched, contracted, how curved, and so on. There is always a certain amount of guesswork involved, to which experience may lend some reliability. The accompanying illustrations of the pupa (Figs. 100, 101) were prepared from a specimen killed in hot water and thus slightly more than normally extended.

No structures on the pupal head appear to be characteristic of *Dolichopeza* alone. The shape and position of the eyes and antennal sheaths, the rather triangular labrum, and the generally-flattened aspect of the entire head are typical of pupae of the sub-

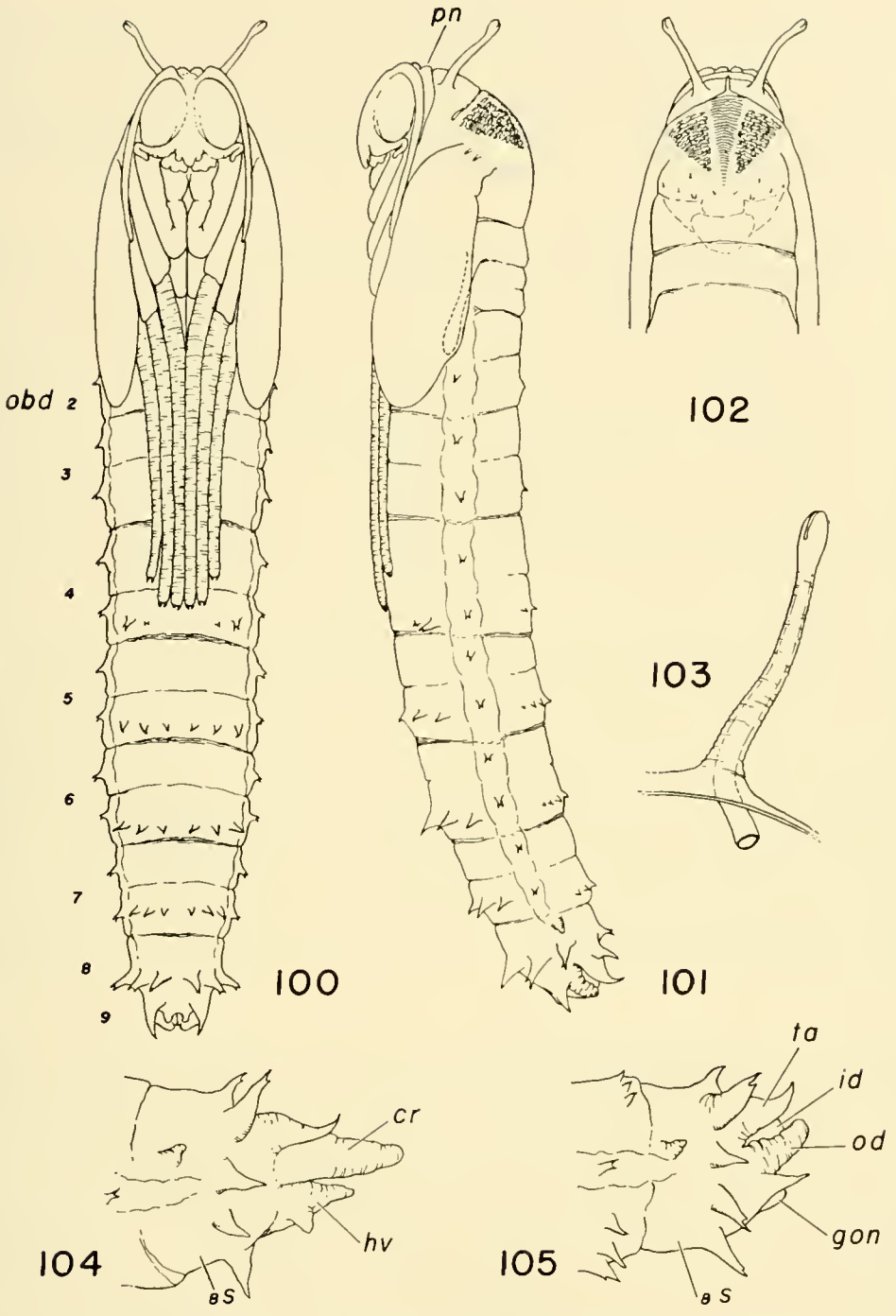


FIG. 100. Pupa of *Dolichopeza (Oropeza) walleyi*, ventral aspect, indicating abdominal segmentation; abd—abdominal segment. FIG. 101. Same as 100, left lateral aspect; pn—pronotum. FIG. 102. Same as 100, dorsal aspect of thorax. FIG. 103. Mesothoracic respiratory horn of *Dolichopeza (Oropeza)* sp. FIG. 104. Cauda of pupa of *Dolichopeza (Oropeza)* sp., female, left lateral aspect; cr—cercus, hv—hypovalve, 8s—eighth sternum. FIG. 105. Same as 104, male; gon—gonapophysis, id—inner dististyle, od—outer dististyle, ta—tergal arm, 8s—eighth sternum.

family Tipulinae. The cephalic crests are small, as in most species of *Tipula*. In having the tips of the sheaths of the maxillary palpi recurved, *Dolichopeza* differs from its nearest North American relatives, *Brachypremma* and *Megistocera*, and from more distantly related *Tanyptera* and *Longurio*, but resembles *Nephrotoma* and most forms of *Tipula*.

Aside from the respiratory horns, the most conspicuous features of the thoracic dorsum of the pupa are two rough-surfaced, reticulated areas (Fig. 102) which are useful in recognition of the genus. However, it should be pointed out that certain species of *Tipula* possess similar reticulated areas on the pupal mesonotum (cf. Alexander, 1920: 977). *Tipula ignobilis*, for example, a species that often occurs in mosses containing pupae of some kinds of *Dolichopeza*, is so marked; but in this species, as well as in the other species of *Tipula* pupae I have seen having such a reticulation on the thoracic dorsum, the pattern of wrinkles extends anteriorly around the bases of the respiratory horns and onto the pronotum. In *Dolichopeza*, on the other hand, the reticulation is confined to the mesonotal cuticle posterior to the pseudosuture, where it occurs as roughly triangular areas in the subgenus *Oropeza* (but weakly developed in *subvenosa*) or more oblong patches in *Dolichopeza americana*. The dorsal mid-line of the mesonotum is characterized by a low, anterior carina, behind which are a series of transverse ridges or folds crossing the mid-line in the region between the reticulated areas.

There are half a dozen pairs of exteremly small spines on the mesonotum, disposed approximately as shown in Figure 102. Takahashi (1958: 121) has found the number of pairs of these spinules useful in distinguishing pupae of certain Japanese species of *Oropeza*, but in the North American species their taxonomic use is impracticable. While at the outermost position, in *Dolichopeza subalbipes*, there are ordinarily two spines together, the pattern for the other species closely resembles that figured. Occasionally a spine may be broken off or missing altogther, or there may be only one where in the corresponding position on the other side two occur together.

The metathorax is narrow and, where exposed dorsally, rather closely resembles the first abdominal segment. Only the proximal ends of the sheaths of the halteres are exposed, in the subgenus *Oropeza*, the remainders being normally concealed beneath the wing sheaths. In *americana*, however, the sheaths of the halteres

are fully exposed but closely applied to the posterior edges of the wing sheaths.

Close behind the head is the very narrow prothorax, which in this genus is distinctly separated from the mesothorax. The respiratory horns, which are of rather uniform shape throughout all the species and which are ordinarily referred to in literature on the Tipulidae as "pronotal breathing horns," are not situated upon this prothoracic segment. Alexander (1920: 752), describing the tipulid pupa in general, said: "Immediately behind the head on the pronotum are the two breathing horns. . . ." In the taxonomy of pupae of Tipulidae, the term "pronotal breathing horns" persists even to the present time (see, for example, Wood, 1952: 81, etc.). The respiratory horns, however, are situated on the pupal mesonotum, between its anterior margin and the pseudosutures (which in the adult are indicated by the pseudosutural foveae, or humeral pits). Dissection of the pupa when the developing adult within is fairly well formed clearly shows the relationship of parts of the imaginal thorax to the areas of the pupal thorax as here identified. Furthermore, the tracheal tube leading from the respiratory horn connects to the mesothoracic spiracle of the developing adult.

A most peculiar difference exists between pupae of *Dolichopeza polita* and all the other North American species of the genus in the appearance of the tracheal connection between the respiratory horn and the spiracle. In most species, this tube is rather straight, making a direct connection, while in *polita* it is greatly convoluted and folded back upon itself, its length easily twice the distance from the base of the breathing horn and the spiracle (Fig. 107). This condition is found in all three races of *polita*. The only other occurrence known to me is in the pupa of *Dolichopeza* (*Nesopeza*) *geniculata* Alexander, which I found projecting from a growth of liverwort on the slope of the volcanic peak, Halla San, on Cheju Island, Korea, in the fall of 1954. I know of few other characteristics in any stage of *Dolichopeza* that so completely set apart one species from all others in a continental fauna.

The first abdominal segment of the pupa is short and indistinctly divided, while the next six segments are formed of broader, well-marked basal and caudal, or anterior and posterior portions. The basal rings lack spinous processes on the dorsal and ventral surfaces but have these present on the pleural folds. The posterior rings bear, in addition to the pleural spinous processes, transverse rows of more or less conical projections, in varying numbers, on the dorsal

surfaces of all segments and the ventral surfaces after the third or fourth segment. The eighth abdominal segment is not differentiated into rings. It bears four * large, subconical, spine-tipped projections on its sternal surface and four slightly smaller ones dorsally, and it has the pleural spinous process present only in the "posterior ring" position. On the dorsolateral surfaces of the eighth abdominal segment, near its anterior edge, there are two low, blunt lobes, one at each side. Unlike the other projections of the pupal abdomen, these lack spinous tips and apparently are homologous with the fleshy lobes occurring in a similar position in the larva. This supposed homology seems correct, inasmuch as the lobes described are characteristic of pupae of species of *Oropeza* but do not occur in *Dolichopeza americana.* These lobes are lacking also in other genera of the Tipulinae, so that the same feature, in a sense, can be used to separate both larvae and pupae of *Oropeza* spp. from those of *Tipula, Nephrotoma* and allied genera.

Sheaths of the various hypopygial elements of the adult comprise the greater part of the caudal segment of the pupa. In the female these (sometimes termed the acidotheca) rather closely resemble the terminal abdominal structures of the adult (Fig. 104). In the male pupa (Fig. 105) the sheaths bear less resemblance to imaginal structures, although the relationship of corresponding parts is clear. Comparison of Figures 111 and 112 shows a conspicuous difference between male pupal terminal structures of *Dolichopeza americana* and species of *Oropeza.* The base of the sheath of the outer dististyle is adjacent to that of the tergal arm in *Oropeza* spp. (Fig. 111), but these two structures are distinctly separated basally in *americana* (Fig. 112). The differences in spinous tips of the caudal sheaths and projections of the eighth segment apparent in these two figures are not reliable for subgeneric recognition, as there is too great an amount of variation in these parts.

Recognition of species in the pupal stage of *Dolichopeza* would seem, from a cursory survey of structures, to be a fairly easy undertaking. The unfortunate truth is, however, that very little can be salvaged for taxonomic use at the species level from the described array of bristles, spinous projections and other apparently taxonomically useful features. With only a scattering of species or a small number of specimens at hand, one might soon find some character in which the available pupae differ. Complications ordinarily arise, however, when larger numbers of specimens are examined,

* Rarely will this number vary, but see Figure 38.

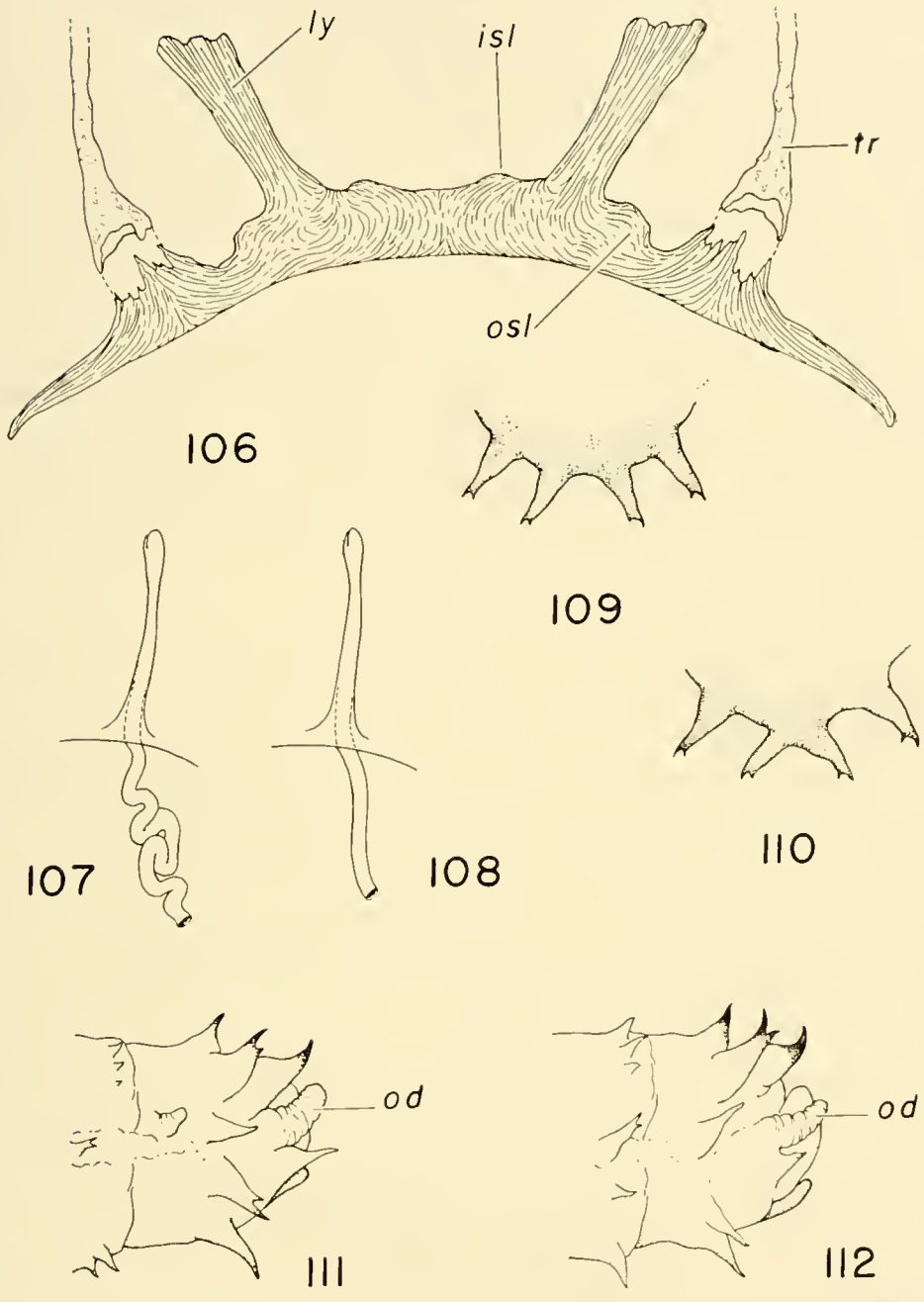


FIG. 106. Spiracular yoke of pupa of *Dolichopeza (Oropeza) similis;* isl—inner secondary lobe, ly—lobe of yoke, osl—outer secondary lobe, tr—larval tracheal trunk. FIG. 107. Mesothoracic respiratory horn and tracheal connection to spiracle in *Dolichopeza (Oropeza) polita* sspp. FIG. 108. Same as 107, *Dolichopeza (Oropeza) trideuticulata.* FIG. 109. Arrangement of spinous processes of eighth abdominal sternum of pupa of *Dolichopeza (Oropeza) sayi* group. FIG. 110. Same as 109, *Dolichopeza (Oropeza) obscura* group. FIG. 111. Cauda of male pupa of *Dolichopeza (Oropeza)* sp., left lateral aspect. FIG. 112. Same as 111, *Dolichopeza (Dolichopeza) americana.*

especially when these represent species of a very uniform group. In some characters, like the bristles of the mesonotum already mentioned, there is too much uniformity throughout the genus, while in others there is as much variation within one species as there is among species. An example of the latter is the number of spine tipped projections on the fifth, sixth and seventh abdominal sterna. The count of these conical points may vary from species to species and from row to row; but on one species, the count of projections in a certain row was found to vary from 8 to 13, complicated by partial fusions, branching, irregular spacing and unusual sizes of projections. As a further example, the spinous projections of the eighth abdominal segment may be single or multiple tipped and may be hooked and variously provided with bristles; but an examination of variation in the tip of a particular projection in a single species showed that the tip varied from two to four branched and that bristles were either present or absent.

One species group within the genus can, however, be separated on the basis of characteristics of the pleural spinous processes. In *Dolichopeza carolus, dorsalis, obscura* and *subalbipes,* these processes are rather blunt-tipped, with an apical bristle that nearly equals the length of the subconical, basal part of the process. In the remaining species, these processes have bifid tips, one of the branches usually short, the other longer and very sharp, with the apical bristle arising in the notch between the two points. Species in the *obscura* group usually have the two medial projections of the eighth sternum originating from a common base or with their bases contiguous (Fig. 110), while in the *sayi* group these projections are ordinarily spaced apart, their bases not touching (Fig. 109). This character is not wholly reliable, exceptions having been seen, but it applies in general. Another character that is nearly always reliable is the presence or absence of spinous projections on the posterior ring of the fourth abdominal sternum. In certain species, these are present and from half to nearly equal the size of those on the fifth segment, whereas in the other species they are absent altogether or represented only by bristles.

One additional character, of a completely different sort, permits separation of species when used in conjunction with the group characters just noted. To my knowledge, this character has never been observed prior to this study and consequently is new to the classification of crane fly pupae. Just posterior to the median projections of the eighth abdominal tergum, there is an infolding of the pupal skin, a sort of pouch or pocket, flattened dorsoventrally, situated

with its closed end directed cephalad in such a way as to be rather readily visible through the eighth tergum, especially in cast pupal skins immersed in alcohol. Microscopic examination of this structure reveals that tiny "stress lines" in the surrounding pupal cuticle converge into the pocket and that the remains of the larval spiracles are attached to the strongly sclerotized arch formed by the converging folds of cuticle (Fig. 106). Although I have not studied the development of this pouch, it seems to be intimately associated with, perhaps a result of, the withdrawal of the larval spiracles at the time of pupation, when the tracheal outlet shifts from a caudal to thoracic position. Since the entire structure seems to me to act as a rigid bar connecting the two spiracles and bringing about their coincident displacement, I have suggested the name "spiracular yoke" for the pouch and related cuticular thickenings at its sides (Byers, 1958: 136). The spiracular yoke in both males and females has a characteristic shape, within limits, for each species, and a study of many specimens indicates that certain features of the yoke are reliably constant. Figures 113 through 124 show something of the variation of the spiracular yoke from species to species. It is not practicable to attempt to describe the variation within each species, but it should be pointed out that the illustrations provided are composites, each based upon several pupae. In the key, reference is made only to the general form of the yoke, such as whether its lobes are elongated or short and whether there are inner, secondary lobes (Fig. 106, isl). I have observed the spiracular yoke also in other genera (*Brachypremna, Megistocera* and several species of *Tipula*), where it is again distinct for the species examined. Perhaps it will prove to be a character of general application in the classification of the pupae of Tipulidae.

TENTATIVE KEY TO PUPAE OF NORTH AMERICAN *DOLICHOPEZA*

Pupae are most easily studied in alcohol. Pupal skins preserved dry should be soaked a few minutes in alcohol, then cleaned of adhering moss particles, soil and other debris before being studied. Skins thus prepared may be flattened with a blunt needle so that the spiracular yoke is seen in the proper profile. Whole pupae may require removal of the eighth and ninth abdominal segments, which separate easily from the imaginal tissue after the fourth day of the pupal stage. Adult genitalia thus exposed may identify the species; the spiracular yoke, at any rate, is made more readily visible. Live pupae, given a few days, will provide their own identification.

113 114 115

116 117 118

119 120 121

122 123 124

FIGS. 113-124. Spiracular yokes of pupae; 113—*Dolichopeza (Dolichopeza) americana*, 114—*Dolichopeza (Oropeza) carolus*, 115—*Dolichopeza (Oropeza) dorsalis*, 116—*Dolichopeza (Oropeza) obscura*, 117—*Dolichopeza (Oropeza) polita*, 118—*Dolichopeza (Oropeza) sayi*, 119—*Dolichopeza (Oropeza) similis*, 120—*Dolichopeza (Oropeza) subalbipes*, 121—*Dolichopeza (Oropeza) subvenosa*, 122—*Dolichopeza (Oropeza) tridenticulata*, 123—*Dolichopeza (Oropeza) venosa*, 124—*Dolichopeza (Oropeza) walleyi*.

The following key is limited in several respects. The pupal instar of *Dolichopeza johnsonella,* as well as that of the two new species described herein, is unknown. Probably *johnsonella* will "key out" near *subalbipes.* Pupal skins identified as those of *carolus* and *subvenosa* were not obtained from reared specimens but were identified on the basis of circumstantial evidence, as explained later under the respective species headings. Only four female pupal skins thought to be of *subvenosa* and three male and three female skins regarded as of *carolus* were found. The pupae of *dorsalis* and *similis* are known from only about half a dozen specimens each, but of the remaining species several to many pupae have been found and studied.

1. Reticulated areas of mesonotum oblong in shape; no blunt lateral lobes on anterior portion of eighth abdominal tergum; spiracular yoke roughly triangular in shape and weakly sclerotized except at edges (Fig. 113) ..... *americana*

   Reticulated areas of mesonotum triangular in shape; a blunt lateral lobe anteriorly on each side of eighth abdominal tergum; spiracular yoke variously shaped, usually with two conspicuous lobes, strongly sclerotized throughout 2

2. Tracheal tube connecting respiratory horn with adult spiracle strongly convoluted ..... *polita* sspp.

   Tracheal tube straight 3

3. Pleural spinous processes of second through seventh abdominal segments blunt-tipped, bearing a single apical bristle about as long as basal portion of process 4

   Pleural spinous processes of second through seventh abdominal segments mostly bifid at tip, with at least one sharply-pointed branch and with apical bristle arising from notch between branches 7

4. Middle projections of eighth abdominal sternum set apart so that the four are about evenly spaced (Fig. 109); spiracular yoke shallowly and irregularly emarginate, the lateral lobes shorter than their width at base (Fig. 115) ..... *dorsalis*

   Middle projections of eighth abdominal sternum set closer together than distance from either to outer projections, or divergent from a low base common to both (Fig. 110); spiracular yoke relatively deeply emarginate, the lateral lobes longer than their width at base, 5

5. Lobes of spiracular yoke only about one and a quarter to one and a half times as long as their width at base, their tips variously rounded; emargination between lobes usually smoothly curved (Fig. 116) ..... *obscura*

   Lobes of spiracular yoke from one and a half to three times as long as their width at base, their tips irregularly truncated, often expanded and notched; emargination between lobes more angular or irregular 6

6. Basal part of spiracular yoke deep, or thick, the emargination between lobes irregular by reason of inner secondary lobes (Fig. 114); middle projections of eighth abdominal sternum clearly separated

at base; spinous projections on fourth abdominal sternum present, about one-third to one-half as long as those on fifth sternum; projections on fifth through eighth sterna very darkly tipped . . . *carolus*

Basal part of spiracular yoke usually shallow, or slender, the emargination between lobes not interrupted by secondary lobes (Fig. 120); middle projections of eighth abdominal sternum set very close together or arising from low base common to both (Fig. 110); usually no spinous projections on fourth abdominal sternum, those of fifth through eighth sterna not all darkly tipped . . . . *subalbipes*

7. Middle projections of eighth abdominal sternum set close together or divergent from a low base common to both (Fig. 110); spiracular yoke broadly and shallowly emarginate, the lobes shorter than their width at base, sometimes with an apical papilla (Fig. 122), *tridenticulata*

Middle projections of eighth abdominal sternum set apart so that the four are about evenly spaced; lobes of spiracular yoke slightly to much longer than their width at base 8

8. Spinous projections on fourth abdominal sternum usually conspicuous, about one-half as long as those on fifth sternum, or longer 9

Spinous projections on fourth abdominal sternum usually inconspicuous or absent, sometimes represented by bristles 11

9. Lobes of spiracular yoke only about one and a half times as long as their width at base, often bluntly rounded at tips; emargination between lobes rather smoothly curved (Fig. 124) . . . . . *walleyi*

Lobes of spiracular yoke about twice as long as their width at base, their tips usually slightly expanded and notched; emargination between lobes more angular, often irregular due to presence of inner secondary lobes 10

10. Reticulation on mesonotum distinct, occurring in roughly triangular areas; spiracular yoke as in Figure 123 . . . . . *venosa*

Reticulation on mesonotum obscure, mostly in form of low, transverse wrinkles or folds similar to those along mesonotal mid-line; spiracular yoke as in Figure 121 . . . . . *subvenosa*

11. Lobes of spiracular yoke about three times as long as their width at base; emargination between lobes deep and angular, with small inner secondary lobes; basal portion of yoke slender, not thick (Fig. 119) . . . . . *similis*

Lobes of spiracular yoke one and a half to two times as long as their width at base; emargination between lobes angular, sometimes irregular due to inner secondary lobes, but not deep; basal portion of yoke thick (Fig. 118) . . . . . *sayi*

PUPAE—NATURAL HISTORY

In nearly all rearing experiments, the length of the pupal stadium in *Dolichopeza* was six days, which is about average for the Tipulidae generally. Occasionally the period was found to be seven days, and one female of *Dolichopeza venosa* spent eight days in the pupal condition, indoors, but did not emerge normally and died in the process. In the laboratory, the time of emergence was artificially

altered, that is to say postponed, by exposure of pupae to bright light or to chilling. It therefore seems reasonable to believe that naturally occurring fluctuations in environment could effect changes in the length of time that the fully formed adult insect within the pupal skin would remain there. It would be interesting to know, for example, whether *Dolichopeza* adults emerge at the end of a six-day pupal stadium, if that time happens to coincide with an all-night rainstorm.

Although it is essentially in a resting state, in which many larval structures disintegrate and the adult anatomy takes shape, the pupa is capable of considerable activity at nearly any time during its existence. Vital physiological activities of the insect must, of course, proceed without interruption; and even as it frees itself of the last larval skin the pupa may be seen to have already a fully-formed and functioning tracheal system and a regularly-pulsating dorsal vessel, both visible through the smooth, pale integument. Pupal activities in ecdysis show that at least a part of the muscular system also is already in operation. In the absence of artificial stimulation, however, the pupa usually remains quiescent, only occasionally wriggling to the opening of its tube and perhaps projecting slightly from it. This movement is accomplished by dorso-ventral undulations of the abdominal segments behind the tips of the wing sheaths, which by their stout spinous projections gain a firm hold in the moss.

Since the pupa lives in the same microhabitat as the larva, little comment needs to be added concerning its general ecology. Each pupa lives in isolation within a burrow often scarcely more than half again as long as the pupa itself. Where moss habitats have been favorable for the development of several larvae, the pupal burrows may be numerous and often crowded, as for example at one place where I found three pupal skins of *Dolichopeza polita* ssp. projecting from one square centimeter of moss surface.

Predation and parasitism.—The relatively defenseless pupae would seem to fall easy prey to several kinds of predators that live in mosses or feed rather generally over the surface of the ground. Only once, however, did I actually find evidence of predation on a *Dolichopeza pupa.* As I was examining a rearing dish, I saw a pupa of *Dolichopeza similis* come wriggling up out of the moss in a most hurried manner. When I saw that its two posterior segments had been nearly torn away, I probed its tube in the moss and discovered a twenty millimeter larva of some species of Elateridae.*

* Alexander (1920:729) reports elaterid larvae feeding on a dead larva of *Tipula trivittata.*

Larvae of *Bittacus apicalis* (Mecoptera) found foraging in moss containing pupae of *Dolichopeza americana* and *polita* were probably seeking only dead pupae or other such decomposing material, as they fed readily on dead pupae and refused living ones when both were offered as food.

Several instances of parasitism of pupae by chalcidoid wasps were noted in the course of rearing experiments. At first, the infested pupae were found dead, broken open at one or more places, with half a dozen or more tiny, spindle shaped larvae busily consuming both the pupal contents and the necrotic edges of the openings in the skin. These larvae were about two millimeters in length, pale at the ends, with a broad, pale spotted band of tan showing through the smooth, transparent skin of the middle region. It appeared that these larvae were only scavengers, there being no direct evidence of parasitism. Yet I wondered why the number of them feeding on any one pupa was always about the same and why they were never found feeding on dead larvae in the same rearing dish.

Attempts to rear these supposed parasites invariably failed, until on 11 June 1952 I found in one of my dishes a newly-formed pupa of *Dolichopeza walleyi,* through the pale integument of which I could see the familiar larvae at work. Inspection showed that the pupal skin was intact, making it clear that the larvae were indeed parasitic. It seems that the parasites must remain very small throughout the larval life of their host and then develop rapidly as soon as the pupa is formed, for, although there is no interference with the process of pupation, by the time the pupa is only a day old it is largely hollowed out by the parasites. By 14 June, activity within the pupal skin had ceased, and two days later the whitish pupae of the wasps could be seen. On 17 June, the reddish eye pigment of the parasites became visible, and between evening of 19 June and morning of the next day there occurred an abrupt change in color of the parasites, the eyes turning deep red and the bodies nearly black. Between 10:00 a. m. and 3:30 p. m. on 23 June, about a dozen tiny wasps emerged through a small hole in the side of the fly pupa. These were identified by Dr. B. D. Burks of the U. S. National Museum as belonging to an undescribed species of *Tetrastichus* (Hymenoptera: Eulophidae).

Similar wasps were subsequently reared from a pupa of *Dolichopeza americana,* in which instance, however, there were only seven parasites. Other species of *Dolichopeza* parasitized by *Tetrastichus* sp. include *obscura* and *subalbipes.* All cases of infestation by this

parasite were observed in May and June, but there is as yet no reason to suspect that pupae of the fall generation are not also parasitized. Rogers (1933: 35) reports braconid parasites in the pupa of *Dolichopeza walleyi* (as *Oropeza sayi*); however, as none of these wasps was preserved, there is no way to be sure whether what he actually observed were also *Tetrastichus*.

It seems probable that the mites often found on adults of *Dolichopeza* congregate on the pupa and attach themselves to the body of the imago as it emerges from the pupal skin.

Pupal development.—The newly-formed pupa is pale tan in color, often with a greenish tinge showing through, especially from the abdominal contents. The dorsum of the thorax is usually a slightly darker tan or brown than is the rest of the pupa, and the thoracic respiratory horns are quite dark brown from the outset of pupal life. During the first few hours of the pupal stadium, the eyes are pale, but the violet-purple pigment of the developing ommatidia within slowly diffuses across, beneath the pupal eye covering, so that at the end of the first day the pupal "eyes" are fully colored and have a brick red appearance. As the individual lenses of the developing adult eye are clearly visible through the pupal skin, it may be seen that the compound eye does not initially form directly beneath the pupal eye cover but is displaced slightly anterolaterally. Within the wing sheaths, the veins sometimes glisten as if filled with air, and the membrane appears as a dark, strongly-convoluted, compactly-folded mass.

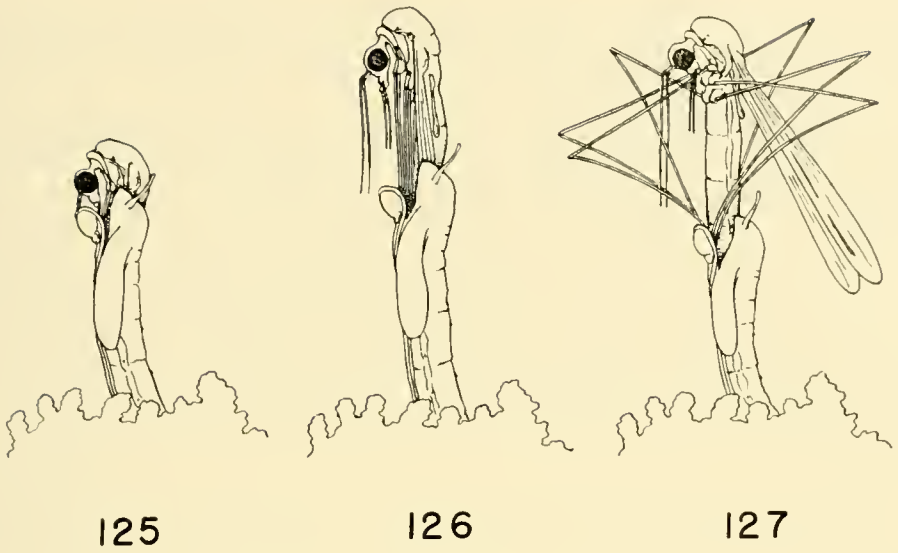
As the pupa grows older, its colors become darker, the greenish hue of the abdomen being replaced by brown in most species of *Oropeza* but remaining in *americana* and to a lesser extent in *dorsalis* and *subalbipes*. The thoracic breathing horns become very dark brown with black tips, and the low median carina of the mesonotum takes on a black color in many species. As the adult body takes shape, some parts of the pupal skin are left apparently empty, or nearly so, by the contraction of the initially rather amorphous tissue of the young pupa into the smaller and more compact adult structures. The hypopygial elements largely pull out of their formative sheaths, and the rostrum, maxillary palpi, antennae and other parts loosen from their sheaths, so that by the end of about four days of the pupal stadium the developing adult is separated almost completely from its pupal covering.

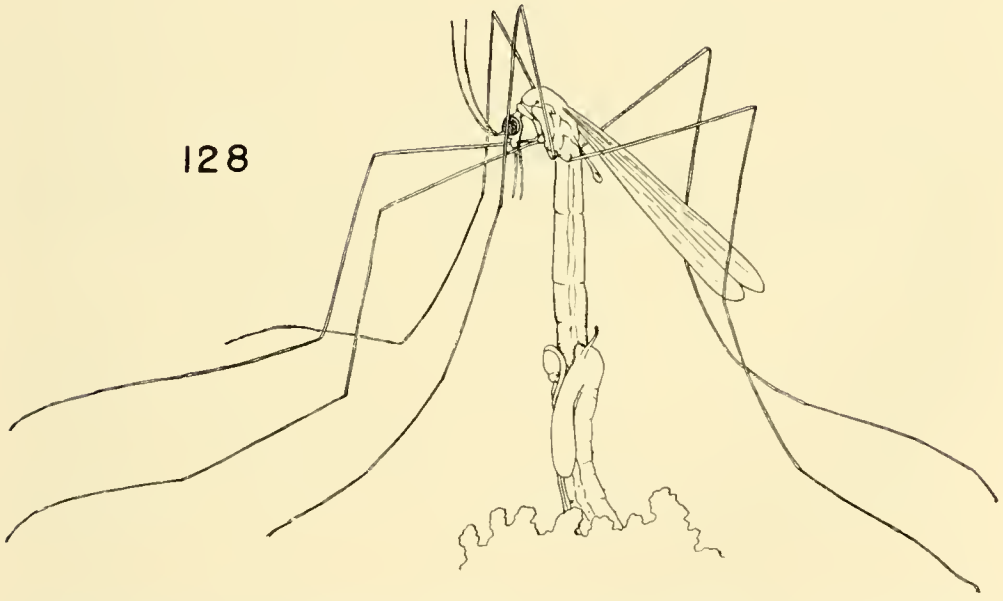
Very marked changes in over-all appearance are undergone by the pupa shortly before the adult is to emerge. When the pupal skin grows rapidly darker brown in color and becomes dry and

shiny, emergence of the adult may be expected within the following eight to twelve hours. At this time, the coloration especially of the head, thorax and wing and leg sheaths becomes noticeably darker, somewhat resembling dark amber-brown glass. Eye color changes from brick red to almost black in only a few hours. On the surface of the wing sheaths, the characteristic pattern of venation of the adult wing, in miniature, can easily be made out in reflected light. In the laboratory, pupae often moved one-third to half out of their tubes at the onset of this drying and darkening period, but I have not been able to verify that they do so under natural conditions.

Emergence of adult.—Emergence of the adult is a rapid process, requiring only a few minutes. I have twice had the good fortune to observe emergence from its earliest moments, when the pupal skin first began to split, and have witnessed by far the greater part of the process on several other occasions. In preparation for emergence, the pupa moves out of its burrow far enough to expose the anterior one-third to one-half its length. After a time, the pupal skin parts in two places: a transverse split between the antennal sheaths and the pronotum, from the mid-line behind the head down to the sheaths of the front legs, and a longitudinal split along the dorsal mid-line, across the occipital portion of the head, the prothorax and the mesothorax almost to the metathorax.* Then, for a few seconds, the adult insect, still fully encased, swallows air in order to expand and lengthen its body. Air is taken into the abdominal part of the ventriculus but much more extensively into the membranous crop, which in one fly killed a few seconds after emergence was found distended so as to fill the abdomen back to the anterior edge of the fifth segment. As a consequence of this inflation, the adult body rises from the pupal skin rapidly and without apparent exertion, until the wings are drawn free of their sheaths, the femora are fully exposed, and approximately the anterior half of the abdomen has emerged (Figs. 125, 126). Although the compressed neck quickly extends, the head remains bowed, with the antennae and maxillary palps directed downward. The wings are not withdrawn as crumpled structures but, somewhat in the manner of an opening parachute, spread to their full expanse as fold after fold of the membrane is drawn taut by the pull from outside. During the minute or less that is required for emergence to the point of freeing the wings, almost the only motion noticeable is the slight tugging action of the coxae.

* The coverings of head and antennae are left attached to the rest of the pupal hull by only a thin, membranous skin and sometimes break off as a unit, a sort of mask.





FIGS. 125-128. Successive stages in the emergence of the adult of *Dolichopeza (Oropeza) polita* ssp. from the pupal skin.

With the greater part of its body free of the pupal skin, the fly begins a rocking motion, combining dorso-ventral movements and extensions and contractions of the abdomen. The legs are withdrawn with somewhat less exertion, the joints between femora and tibiae flexed first out to the sides (Fig. 127), then high overhead, as the long tarsi are pulled free. As the legs are freed, the tip of the abdomen remains fast in the pupal skin, the wings are kept folded over the back, and the antennae are directed upward (Fig. 128). Then, with its feet braced against the moss and its wings fluttering weakly, the fly suddenly breaks completely away from its

pupal hull, moves a short distance over the moss surface, and pauses to rest, with legs outspread and the weight of the thorax and abdomen directly on the moss.*

The soft and almost colorless sclerites begin to harden and take on slight color in a matter of minutes, while the body size reduces by discharge of swallowed air and of the last of the copious greenish meconium, the fluid wastes resulting from pupal metabolism. Most of the meconium is expelled during emergence, leaving the pupal skin almost a quarter full of the greenish fluid, unlike the condition found in most Tipulinae, which leave their pupal skins empty. It may be a quarter of an hour before the fly attempts to take to the wing, and it seems that in its natural surroundings the newly-emerged fly must be easy prey for all manner of predators that are active at night.† Within two or three hours, the fly is well colored and hardened and is capable of sustained flight. Its full coloration develops in about six to eight hours following emergence, although because of callowness of body the fly may be considered teneral for a longer period of time. With emergence, the life cycle begins anew. Figure 99 summarizes the stages of development, indicates the approximate rate of growth, and illustrates the changes in body size as the insect passes from egg through the larval instars, pupation and emergence as an adult fly.

KEY TO ADULT MALES OF NORTH AMERICAN *DOLICHOPEZA*

1. Wings without discal cell (cell 1st M_2); cross-vein m-cu joining media before its first branching (Fig. 2); ninth tergum without lateral arms (Fig. 129) ..... subgenus *Dolichopeza;* note that the male of *D.* (*D.*) *borealis* new species is so far unknown; see discussion of that species ..... *americana*

   Wings with discal cell normally present; cross-vein m-cu joining the media beyond its first branching (Fig. 1); ninth tergum with lateral arms ..... subgenus *Oropeza* 2

2. Gonapophyses shaped like small knobs, bearing decurved, stout black spines and bristles (Fig. 6) ..... *obscura* group 3

   Gonapophyses with tips flattened and blade-like or slender and pointed, sometimes with hairs but never with stout black spines, *sayi* group 10

3. Tarsi white and femora and tibiae pale with narrowly darkened tips; body coloration yellowish marked with dark brown or black; wings with intense brown stigmal spot; ninth tergum as Figure 208 or 209 ..... *subalbipes*

* In instances of emergence from pupae in mosses on the undersides of rock ledges or on vertical surfaces, some variation of the described procedure is of course necessary. Such conditions, however, were not duplicated in the laboratory.

† Emergence in the laboratory usually occurred in the early hours of darkness, between 9:00 p. m. and midnight.

Tarsi dusky, brown, yellowish brown or yellowish white, but tips of femora and tibiae not contrastingly darkened; body coloration brownish with dark brown markings 4

4. Apical two-thirds of tarsi yellowish white, grading into light brown on basal third; medio-posterior margin of ninth tergum with two broad, rounded lobes and a slightly longer central tooth (Fig. 137) *australis*

Tarsi uniformly colored throughout, dusky, brown or yellowish brown and not conspicuously paler than legs 5

5. Medio-posterior margin of ninth tergum undulating, with two broad, rounded lobes; tergal arms slender and not much expanded at tips (Fig. 157); a median brush of black hairs on eighth sternum (Fig 162) ..... *johnsonella*

Medio-posterior margin of ninth tergum with projecting teeth; tergal arms various; no brush of hairs on eighth sternum 6

6. Tergal arms widely flared and emarginate at tips; teeth of ninth tergum not set close together (Fig. 164) ..... *obscura*

Tergal arms not flared or emarginate at tips; teeth of ninth tergum set close together, usually on a common basal projection 7

7. Outer dististyles blunt-tipped and not expanded at bases; median lobe of tergal margin subrectangular in shape, bearing three teeth of nearly equal length (Fig. 221) ..... *tridenticulata*

Outer dististyles with pointed tips and with basal portion usually enlarged; median lobe of tergal margin various but usually with three teeth, the central one the longest ..... *polita* subspecies 8

8. Thoracic dorsum shiny or "polished"; basal enlargement of outer dististyle darkened around the edge; median lobe of tergal margin usually slender but may vary (Fig. 171) ..... *polita polita*

Thoracic dorsum dull and opaque, rarely slightly shiny in certain lights; basal enlargement of outer dististyle pale; median lobe of tergal margin usually distinctly three-toothed 9

9. Three teeth of median lobe of nearly equal length, the middle one slightly the longest, and all set close together; tergal arms flared about mid-length and tapering to slender tips (Fig. 188), *polita cornuta*

Three teeth of median lobe variable in length, middle tooth the longest, but teeth not always set close together; tergal arms only slightly expanded at tips but widest there (Fig. 180) ..... *polita pratti*

10. Outer dististyles pale, shorter than inner dististyles, not conspicuously projecting (Fig. 145); tarsi white and femora and tibiae pale with narrowly darkened tips ..... *carolus*

Outer dististyles dark or yellowish, longer than inner dististyles and conspicuously projecting; tarsi yellowish white, tan, gray or brown 11

11. Gonapophyses narrow, tapering to blackened, heavily sclerotized points; tergal arms broadly expanded and spatulate at tips; medio-posterior margin of ninth tergum with a broad, irregular projection 12

Gonapophyses not narrow and tapering to points; tergal arms and margins various but not as above 13

12. Adminiculum with a prominent, subapical, posterior (or ventral) spine (Fig. 219) ..... *subvenosa*
Adminiculum without a subapical spine (Fig. 234) ..... *venosa*
13. Ninth tergum very shallowly emarginate, with undulating margin; tergal arms not expanded at tips (Fig. 149); gonapophyses short, terminating in an abrupt, spinous tip (Fig. 152) ..... *dorsalis*
Ninth tergum slightly to moderately emarginate and toothed; tergal arms slightly to markedly expanded at tips; gonapophyses longer than broad, variously expanded at tips 14
14. Gonapophyses slightly widened toward the tips, the margins entire; tergal arms only slightly expanded at tips (Fig. 195) ..... *sayi*
Gonapophyses expanded at tips, the margins irregularly toothed; tergal arms markedly expanded at tips 15
15. No prominent projections from inner faces of gonapophyses; adminiculum without spines at tip (Fig. 241) ..... *walleyi*
A long, spinous projection directed dorso-cephalad from the inner (anterior or dorsal) face of each gonapophysis; adminiculum with two small apical spines (Fig. 204) ..... *similis*

KEY TO ADULT FEMALES OF NORTH AMERICAN *DOLICHOPEZA*

1. Wings without discal cell (cell 1st M_2); cross-vein m-cu joining media before its first branching (Fig. 2) ... subgenus *Dolichopeza* 2
Wings with discal cell normally present; cross-vein m-cu joining the media beyond its first branching (Fig. 1) .. subgenus *Oropeza* 3
2. Hypovalves of ovipositor each with a heavily sclerotized apical tooth (Fig. 135); tarsi white from mid-length of first segment to apex of fourth ..... *americana*
Hypovalves of ovipositor tapering evenly to tip (Fig. 136); only about apical one-sixth of first segment and all of second segment of tarsi pale (white in hind tarsi only), third segment dusky, fourth and fifth dark ..... *borealis*
3. Tarsi white; tibiae and femora pale in color, their tips conspicuously darker and sharply contrasting 4
Tarsi dusky, yellowish brown, or brown; or, if whitish, without darkened, contrasting tips on tibiae and femora 5
4. A heavily sclerotized spot, conspicuously darker than the tip or any other part of the hypovalve, present on each side of eighth sternum (Fig. 148), approximately below the ninth or base of the tenth tergum ..... *carolus*
No such spot present, although entire eighth sternum and hypovalves may be uniformly strongly sclerotized; or spot may show weakly, in rare instances, never as strongly sclerotized as tip of hypovalve ..... *subalbipes*
5. Dorsum of thorax contrastingly colored or striped, the darker portions much darker than the pleura; if striped, the stripes distinct; body coloration generally yellowish brown, the abdomen annulated with darker brown or black; legs yellowish, yellow-brown, yellowish white, or brown 6

Dorsum of thorax not contrastingly colored or striped and not conspicuously different in color from pleura; if striped, the stripes indistinct and not much darker than the ground color; general body coloration dusky brown, dark yellowish brown, or light brown, annulated with darker brown in each case; legs dusky, gray-black, dark brown, brown, or brown with pale, yellowish brown tarsi . . . 12

6. Thoracic pleura pale and unmarked (except for slight darkening of the pre-episternum in occasional specimens 7

Thoracic pleura distinctly marked, especially on the anepisternum, ventral part of pre-episternum and mesothoracic meron (see Fig. 14) 8

7. Dorsum of thorax reddish brown in color, sometimes indistinctly striped, with a narrow, cocoa-brown median stripe usually present but not clearly differentiated; flies of bogs, marsh borders and swamplands especially . . . . . *dorsalis*

Dorsum of thorax marked by three distinct, reddish brown stripes on a yellowish brown ground color; principally flies of mesic woodlands, in northern and eastern North America . . . . . *walleyi* (part)

8. Cubital vein scarcely, if at all, more conspicuous than other wing veins (use no magnification); stigmal spot usually not very sharply defined and not intensely colored; flies of mesic woodlands generally south of Virginia, Kentucky and southern Indiana, and west of Illinois, Wisconsin, etc. (cf. 7, above) . . . . . *walleyi* (part)

Cubital vein clearly more conspicuous than any other (use no magnification) by reason of a dark seam of color along the vein; stigmal spot intense, well defined and much darker than the ground color of the wing 9

9. Tenth tergum more strongly sclerotized than cerci or hypovalves, although dark spots may be present on hypovalves and eighth sternum (Fig. 207); stripes of thoracic dorsum brown to dark brown, tending to merge behind middle of prescutum; large flies of yellowish coloration, the wings with a gold-amber tinge . . . . . *similis*

Strongest sclerotization of ovipositor is on hypovalves; stripes on thoracic dorsum dark brown, distinctly separated; wings tinged with light grayish brown 10

10. Legs dark grayish brown, the tarsi light brown; body coloration yellowish with narrow annulations at incisures of abdomen; dark coloration on hypovalves neither very intense nor widespread (Fig. 200); flies of marsh borders and swamps, especially . . . . . *sayi*

Legs pale, the tarsi whitish, yellowish white, or very pale tan; body coloration tan with broad, dark brown annulations at incisures of abdomen; dark coloration of hypovalves intense and generally distributed behind eighth sternum, the posterior margin abruptly paler (Figs. 220, 237); flies of rocky areas and stream borders . . . 11

11. Flies of the Appalachian Mountain region, from northern West Virginia southward through Virginia and North Carolina to northern Georgia . . . . . *subvenosa*

Flies of northeastern United States and Canada, from northern West Virginia northeastward to Nova Scotia and northwestward to Minnesota, Alberta and Yukon . . . . . *venosa*

12. Legs light brown, tarsi fading to pale yellowish brown or yellowish white ..... *australis*
    Legs and tarsi of about the same color, brown, dark brown, dusky or blackish 13
13. Pronotum, prescutum and pleura of thorax markedly lighter in color than occiput of head; antennae with the two basal segments abruptly paler than flagellum 14
    Pronotum, prescutum and pleura of thorax not much, if at all, lighter in color than occiput of head; antennae more unicolorous, or, if basal segments are pale, the flagellar segments gradually becoming darker toward the tip of the antenna 17
14. Wing tinged with golden brown, the stigmal spot darker brown, with lighter areas both before and beyond it; the larger veins also dark brown, with a seam of brown color along veins Cu and m-cu; prescutal stripes usually evident, although poorly defined; abdominal annulations distinct; an intensely sclerotized spot medially on eighth sternum at base of hypovalves (Fig. 163) ..... *johnsonella*
    Wing faintly tinged with light gray or grayish brown, the stigmal spot only slightly darker than the ground color; veins gray to brown, lacking seam of color along Cu or m-cu; prescutum unicolorous or nearly so; abdominal annulations indistinct; no intensely sclerotized spot near base of hypovalves, although hypovalves may be in part strongly sclerotized ..... (*polita* subspecies) 15
15. Thoracic dorsum shiny or "polished" ..... *polita polita*
    Thoracic dorsum usually dull and opaque, light brown or light reddish brown in color 16
16. Flies of Minnesota, western Wisconsin, Iowa, western Illinois, Missouri, Kansas, Arkansas, etc. ..... *polita pratti*
    Flies of Indiana, eastern Illinois, Ohio, Kentucky, southern Michigan, western New York, etc. ..... *polita cornuta*
17. Tenth tergum more densely sclerotized than any other part of ovipositor (Fig. 170); thoracic coloration usually as dark as occiput of head; stigmal spot grayish brown to brown ..... *obscura*
    Subterminal area of hypovalves more densely sclerotized than any other part of ovipositor (Fig. 229); thoracic coloration usually slightly paler than that of occiput; stigmal spot grayish brown ..... *tridenticulata*

Subgenus *Dolichopeza*

Dolichopeza (*Dolichopeza*) *americana* Needham

Literature references.—Dolichopeza americana Needham. Needham, 1908: 210-211, pl. 16 (wing); Johnson, 1909: 117, pl. 15 (wing); Alexander, 1919: 929, pl. 43 (wing); Alexander, 1920: 981-982; Dietz, 1921: 259; Alexander, 1922b: 61; Alexander, 1924: 59; Alexander, 1925: 172; Johnson, 1925: 32; Alexander, 1926: 239; Pierre, 1926: 9; Leonard, 1928: 698; Alexander, 1929a: 236; Alexander, 1929b: 25; Johnson, 1929: 130; Alexander, 1930a: 272; Rogers, 1930: 22; Alexander, 1931a: 138.

Dolichopeza (*Dolichopeza*) *americana* Needham. Alexander, 1936: 279; Alexander, 1940: 618; Alexander, 1941a: 295; Alexander, 1942: 210, fig. 24A (wing); Rogers, 1942: 118; Foote, 1956: 221.

Original description.—"Its expanse of wing is 21 mm. Its color is brownish, paler ventrally. Its antennae are of moderate length, with the brown flagellum consisting of ten segments, slowly diminishing in length toward the tip and beset with a few stout, black hairs. The wings are of pale brown, with venation as shown in the figure just cited (fig. 5 of pl. 16), the halteres are infuscated at tips. The legs are of the usual excessive length; femora and tibiae are brown, with white bases, and all the tarsus is white except the basal half of the first segment and the apical half of the fifth segment."

Types.—No holotype or syntypical series was specifically designated by Dr. Needham, who wrote to me, in August 1951: "The specimens of *Dolichopeza americana* went to the New York State Museum at the conclusion of my third report. Whether they have been preserved or not I do not know; some other material has been lost." No specimens of this species are now in the collection at Albany, so I must assume that the type series is lost or destroyed. However, because *americana* is readily recognized, it seems unnecessary at this time to designate a neotype.

Diagnostic characteristics.—This is the most easily recognized species of *Dolichopeza*, for because of its dusky coloration, long, slender legs and white feet it is not likely to be confused with any other North American crane fly. Although it somewhat resembles *Hexatoma albitarsis* (O. S.), a species that sometimes occurs in the same general habitats, *americana* may be readily recognized in the field by its much longer and more slender legs. Its usual resting posture—hanging from overhead support by the prothoracic legs only, with the wings outspread—is also an aid in field recognition. From the only other known American species of the subgenus *Dolichopeza* (that is, *borealis*), *americana* may be distinguished by its almost completely white tarsi, as well as by certain other color and structural differences discussed under that species.

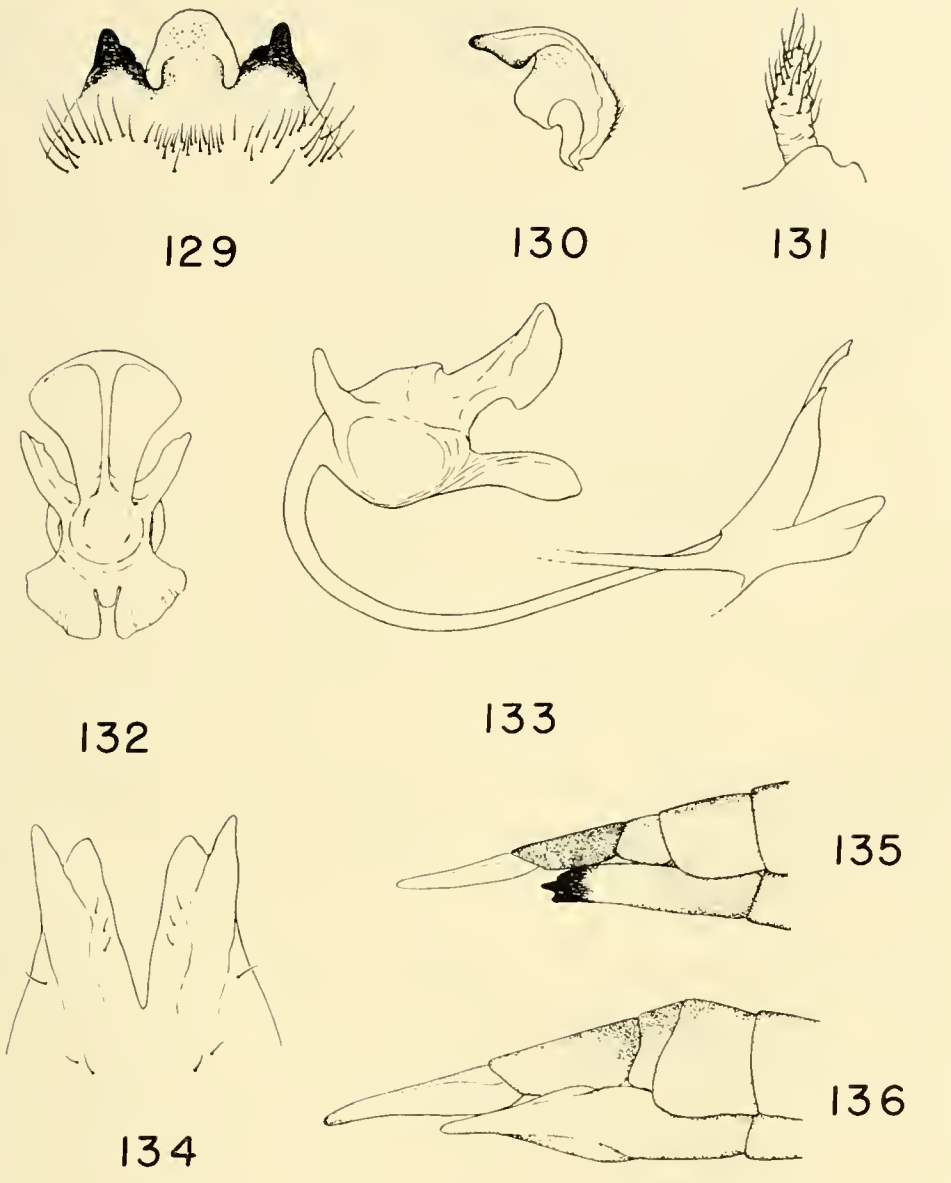
Descriptive comments.—At a distance, *americana* appears to be colored black with white feet, but at close range it is seen to be of a dark brown color dorsally, paler beneath, at the tip of the abdomen, and on the thoracic pleura, which are marked by dark spots on the mesothoracic meron, pre-episternum and anepisternum. The prescutum is indistinctly marked by three longitudinal stripes of a

rich, dark brown color, while the scutellum and postscutellum are abruptly paler than all other dorsal surfaces, being a glossy grayish tan. These and other color markings of the species are frequently obscure on pinned specimens of much age. Membranous areas of the abdomens of newly-emerged females often have a greenish color, which carries over from the larval stage; this is only transitory, however, and gives way in a few days to the characteristic brown.

Venation in *americana* is extremely constant throughout the species' range, only a few abnormalities having been found among more than a thousand specimens examined. Presence of the vein Sc_1 has been noted two times, absence of a section of M_2 has been found twice, and an indication of a vein, in the form of a row of macrotrichia, projecting into cell M_3 has been seen in one specimen. I collected a specimen in North Carolina that had a spurious cross-vein in cell R_3 and in West Virginia one that had a distally directed spur vein from the m-cu cross-vein. One instance of a forked M_3 vein has been seen.

Males vary in over-all length of body from slighty over 7 mm. to about 10 mm., their wings from about 8 mm. to approximately 11 mm., nearly always just a bit longer than the body. Females average somewhat larger, the body 8.5 mm. to 12 mm., wing 8.5 mm. to 12.5 mm. All the smaller specimens were collected in August, while the larger ones were taken in June, mostly from the northern states or high in the Appalachians.

In its hypopygial structure, the male *americana* is markedly different from the species of *Oropeza*, although except for the tergal arms each part in the one finds its counterpart in the other. The ninth tergum is intensely sclerotized, emarginate medially but with a narrow, divided backward projection along the dorsum of the tenth segment (Fig. 129). Into the two deep concavities of the ninth tergum fit the strongly recurved tips of the inner dististyles. There is no *Oropeza* in which the apical portion of the inner dististyles is so reflexed or fits into the sculptured margin of the ninth tergum. The outer dististyles are shorter than the broad, basal portion of the inner dististyles, are pale straw yellow in color, and are covered with fine hairs. Viewed from above, they are slender, but they are somewhat flattened, so as to appear broader when seen from the side (Fig. 131). The gonapophyses are yellowish and are partially fused to form a trough-like backward extension of the ninth sternum (Fig. 133). Adminiculum and penis are pale yellow, less strongly sclerotized than these same struc-



FIGS. 129-135. *Dolichopeza (Dolichopeza) americana;* 129—ninth tergum of male, with tenth tergum projecting from beneath, 130—left inner dististyle of male, dorsal aspect, 131—left outer dististyle, lateral aspect, 132—vesica and its apodemes, dorsal aspect, 133—vesica, penis, adminiculum and gonapophyses, left lateral aspect, 134—hypovalves of female, ventral aspect, 135—terminal abdominal segments of female, right lateral aspect. FIG. 136. Terminal abdominal segments of female *Dolichopeza (Dolichopeza) borealis* new species, holotype, right lateral aspect.

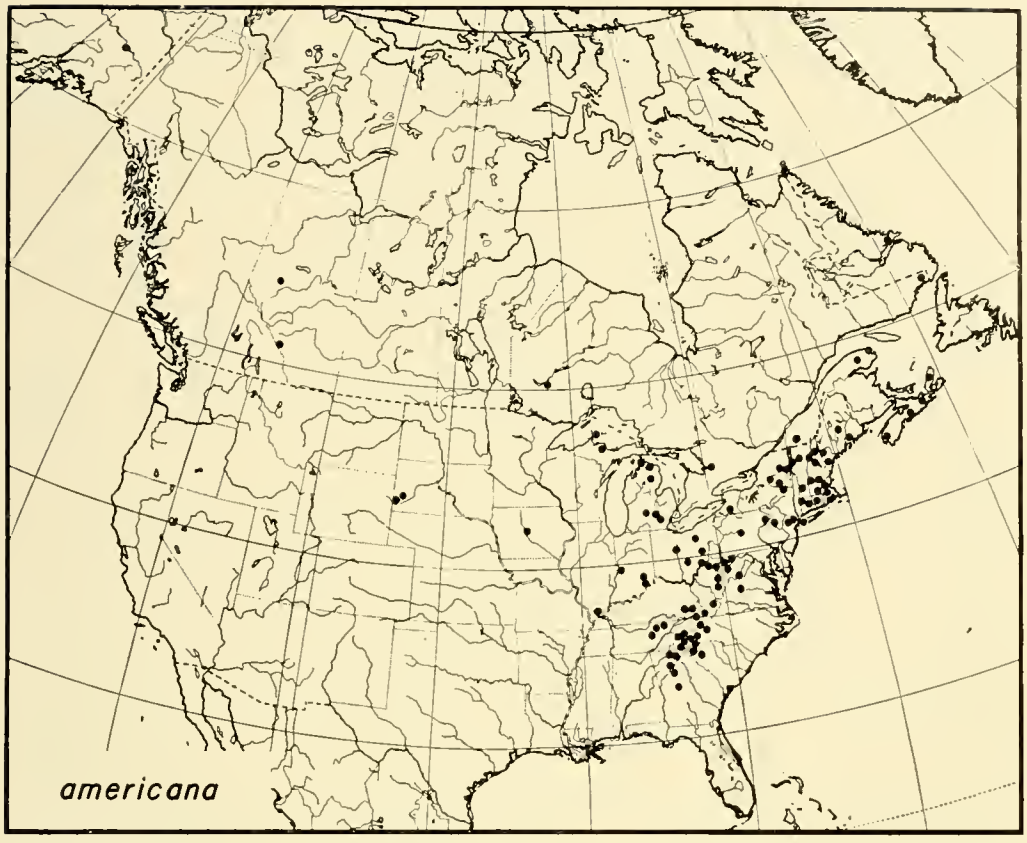
tures in any of the species of *Oropeza.* In comparison with the eighth sternum, the ninth in *americana* is much smaller than it is in any *Oropeza,* suggesting a closer relationship with certain species of subgenus *Nesopeza* in which the ninth sternum is nearly concealed by the eighth.

The ovipositor of the female *americana* is unlike that of any other species of the genus in North America, in that the hypovalves each terminate in a blackened tooth that projects beyond the otherwise truncate end (Fig. 135). Also, the ninth tergum is somewhat longer in this species than in species of *Oropeza* of comparable size.

As described by Needham, the number of antennal segments is twelve. I cannot find any evidence of fusion of the last two segments, in microscope slide preparations of the antennae, but one slide (Haywood County, North Carolina, 30 June 1924, J. S. Rogers) clearly shows thirteen segments, a small apical segment present on each antenna, as is the case in species of *Oropeza.* Alongside the lower edge of each eye, there is a conspicuous black spot. Such a spot occurs also in *Dolichopeza* (*D.*) *albipes* of Europe but is lacking in the only other American species of this subgenus, as well as in *Oropeza.* The significance of these spots is not known to me.

Geographical distribution.—At the outset of this study, the known range of this species included only eastern Labrador and the Appalachian Mountain region southward to northern Georgia, with a westward extension from New York to Michigan. However, *americana* proved to have been well named. It has the most extensive geographic range of any species of *Dolichopeza* in the world, covering over two and a half million square miles of North America, from the range described above westward into the Black Hills of South Dakota and northwestward to Alberta and the central valley of Alaska. There are, however, some wide gaps in this pattern of distribution, due at least in part to insufficient exploration. Just how the Black Hills habitat connects with the rest, if indeed it does, is not clear; this problem is discussed in the conclusions. In the Ozark-Ouachita Mountain region, there are what I regard as favorable habitats for this species, here and there, and perhaps in time the species will be recorded from that area.

Habitats.—Adults of *americana* are most often associated with rocky habitats, such as the limestone or sandstone gorges of Indiana and Ohio, the "rock houses" of the Appalachians and their foothills (Rogers, 1930: 5), and undercut or broken rock along streams in most elevated parts of eastern North America. In the



MAP 1. Range of *Dolichopeza (Dolichopeza) americana* Needham. Each spot represents one or more collections within a county (United States) or at a locality.

northern part of its range, *americana* seems to find the temperature, dampness and deep shade of its southern haunts matched in the cool forests and wet woodlands, although I have never found it to be so numerous in such habitats. Perhaps the reverse is true: that the rocky Appalachian ravines provide the "northern" microclimate in which *americana* can prosper. Individual flies are often found concentrated in small niches where suitable resting conditions prevail. For example, all individuals of *americana* taken on Harney Peak in the Black Hills were found beneath one outcropping rock, and an all-day search of the nearby forest revealed no additional flies. Again, in a southern Illinois locality, a few flies of this species were discovered in a darkened cranny, while a careful inspection of a wide surrounding area proved fruitless.

Seasonal distribution.—In those regions where I have watched and collected *americana*, I have found it the first species of the genus on the wing, both in the spring and late summer generations. In most of Ohio, Indiana and southern Michigan, it may be expected about two or three weeks after the average date of last

killing frost, in the spring. This would place the peak of spring emergence in the areas mentioned at about the first to third weeks of May, depending upon local average climate, and, of course, depending upon the weather of the year. In Washtenaw County, Michigan, a pupa was collected on 13 May. Prolonged observations in a limited area in Turkey Run State Park, Parke County, Indiana, in 1953, showed *americana* present about a week before the first appearance of any species of *Oropeza.* On 18 May, ten single males and two mating pairs were observed; and on succeeding days the numbers of mating pairs increased steadily, reaching a peak of twenty-one pairs on 24 May and thereafter declining steadily. Between 18 and 29 May, only one unmated female was seen, but after 29 May, as the numbers of males diminished, the numbers of single females increased. By 9 June, *americana* had all but disappeared from the particular cranny where these observations were made and from the nearby woods. The spring population generally begins to wane, in this region, in late May to mid-June, or about ten days to two weeks after strong emergence begins, although stragglers may be netted almost any time throughout the summer, and mating pairs may be encountered, now and then, late into June. From the first generation to the second is a matter of only about ten weeks, and a second peak of emergence occurs in the early days of August, continuing for one to two weeks. For data on other parts of the species' range, see the notes on distribution, below.

Immature stages.—Eggs of *Dolichopeza* (*D.*) *americana* measure about .60 mm. x .25 mm., and a single female lays about 110 eggs. The duration of the egg stage is seven days, after which the larvae may reach the fourth instar within twenty-three days.

The larva of *americana* is the most colorful of all North American species of the genus. Its green ground color, brownish black markings and bright green spiracular disc are distinctive characteristics (Fig. 97). Lacking the dorsolateral lobes of the eighth abdominal segment, the larva of *americana* more closely resembles certain species of *Tipula* than it does its nearer relatives in *Oropeza.* It is very similar to the larva of *Dolichopeza* (*D.*) *albipes* of Europe, the only other described larva in this subgenus (see Beling, 1886: 189-191); and it may be that the closely appressed median lobes of the spiracular disc and the peculiar markings of the dorsum are characteristic of the subgenus.

Numerous larval habitats of this species have been discovered.

These vary from rather dry *Tetraphis pellucida* growing together with a powdery lichen on the undercut surface of a sandstone cliff to decidedly damp *Hypnum imponens* growing on rich forest soil beside a small stream. The ability of *americana* to survive in this broad range of habitats probably accounts for its wide distribution and leads me to expect it in many areas where it has so far not been found, such as in the Ozark Mountains. Known larval habitats of this species include, in addition to those mentioned above, *Atrichum macmillani, Leucobryum glaucum, Dicranella heteromalla, Bryhnia graminicolor, Mnium punctatum,* and the liverwort *Plagiochila asplenioides.* All these bryophytes were growing as thin coverings over sandstone cliffs, except the *Bryhnia,* which was collected from a deeply shaded clay-till bank. Feeding habits of the larva of *americana* as compared with those of *Oropeza* larvae are discussed under larval natural history.

In the pupal stage, the color pattern is altered but still very different from any of species of *Oropeza.* The green coloration of the abdominal segments and to some extent the zig-zag dorsal markings are carried over from the larva. The leg sheaths, wing pads, thorax and head pass through shades of tan and brown, eventually becoming nearly black, shortly before emergence of the adult. The cast pupal skin often shows an irregular, marbled pattern of dark brown in the region of the thoracic dorsum; this pattern does not show clearly in the older pupa, although it can be made out when the thorax is paler in color. Morphological characteristics of the pupa of *americana* which distinguish it from pupae of species of *Oropeza* are covered in the section on pupal morphology.

Notes on distribution.—ALASKA—58 miles southeast of Fairbanks (Alaska Highway Milepost 1465), 10 July. ALBERTA—Banff National Park, Banff, 4 July; 39 miles south-southeast of Valley View, 10 July. CONNECTICUT—Hartford County, 8 to 12 June; Litchfield County, 9 to 12 June; Tolland County, 14 June. GEORGIA—Bibb County, 9 June; DeKalb County, 19 August; Fulton County, 25 August to 3 September; Lumpkin County, 23 May; Union County, 10 to 28 June. ILLINOIS—Pope County, 14-15 July. INDIANA—Jefferson County, 22 July to 27 August; Jennings County, 3 August; Parke County, 10 to 25 June, 15 July, and 11 to 30 August. IOWA—Boone County, 26 May. KENTUCKY—Letcher County, 3 July. LABRADOR—Rigolet, 16 July. MAINE—Cumberland County, 1 July; Hancock County, 16 June; Oxford County, 11 July; Penobscot County, 14 June. MARYLAND—Garrett County, 26 June. MASSA-

CHUSETTS—Berkshire County, 13 to 20 June and 19 July; Middlesex County, 11 July; Norfolk County, 11 June; Suffolk County, 11 July. MICHIGAN—Cheboygan County, 2 July; Eaton County, 31 May; Keweenaw County, 25 June; Livingston County, 30 May; Marquette County, 16 July; Oscoda County, 17 June; Presque Isle County, 29 June; Washtenaw County, 12 June. NEW HAMPSHIRE—Carroll County, 4 July; Cheshire County, 16, 19 June; Coos County, July; Grafton County, 29 June and 8 July; Hillsboro County, no date. NEW JERSEY—Bergen County, 5 July; Essex County, June and July. NEW YORK—Albany County, 18 June; Cattaraugus County, 30 June; Essex County, 19 June; Fulton County, 18 June; Hamilton County, 17 to 23 June; Herkimer County, August; Queens County, 22 June. NORTH CAROLINA—Buncombe County, 30 May; Burke County, 14, 21 June and 1 July; Haywood County, 30 June and 29-30 July; Macon County, 11 June and 23 August to 2 September; Swain County, 11 to 19 June and 9 August; Transylvania County, 10 June; Yancey County, 9 to 15 June. NOVA SCOTIA—Guysborough County, 30 June; Halifax County, 29 June; Inverness County, 3 July; Yarmouth County, 27 June. OHIO—Delaware County, May; Harrison County, 5 August; Hocking County, 20 May to 8 June; Portage County, 25 June and 16 August; Washington County, 19 June. ONTARIO—Kenora District, Sioux Lookout, 6 July; Orillia, 10 June. PENNSYLVANIA—Centre County, 25 June and 5 July; Columbia County, 15 July; Luzerne County, 4, 11 to 19, and 27 June and 5 to 10 July. QUEBEC—Bradore Bay (north shore St. Lawrence River), 13 July; Gaspé Peninsula (Mt. Lyell and north shore), 3 July; Knowlton, 26 June. SOUTH CAROLINA—Greenville County, 10 June and 16 July to 30 August; Pickens County, 29 June. SOUTH DAKOTA—Custer County (Harney Peak), 12-13 and 24 July; Pennington County (Horsethief Lake, in Black Hills), 16 and 24 July. TENNESSEE—Blount County, 12 June; Cumberland County, 25 June; Fentress County, 30 May to 24 June, and July and August without dates; Sevier County, 7 May to 13 June, 30 June and 16 September; Scott County, 30 May and 24 July. VERMONT—Chittenden County, 15 to 24 June; Washington County, July. VIRGINIA—Giles County, 5 June to 13 July and 11 to 28 August; Nelson County, 14 August; Rockingham County, 6 July; Smyth County, 20 June; Washington County, 18 August; Wise County, 2 July and 16 August. WEST VIRGINIA—Marion County, 5 August; Pocahontas County, 23 June and 5 July; Preston County, 25 June; Randolph County, 5 July; Tucker County, 24, 25 June; Wetzel County, 5 August.

Dolichopeza (*Dolichopeza*) *borealis*, new species

The following description is based upon a single female, pinned. The specific name refers to the far northern range of the species.

Description.—General coloration dark grayish brown, similar to that of *americana*. Prescutum uniformly dark, without indication of stripes. Scutellum grayish buff as in *americana* but postscutellum dark, not pale as in *americana*. Anepisternum and pre-episternum of mesothorax evenly darkened throughout; that is, without the central pale area found in *americana*. Eyes black. Antennae thirteen-segmented, the terminal segment elongate, about half as long as the penultimate segment; scape and pedicel pale, the flagellum dusky. Wings strongly tinged with grayish brown, the stigmal spot and heavier veins very dark brown. Femora and tibiae dark grayish brown. Approximately the apical one-sixth of each basitarsus is pale, the remainder similar in color to the tibia; the second tarsal segment is pale, white in the hind tarsi but only pale tan to yellowish white (as in *venosa* or *australis*) in the fore and middle tarsi; the third segment darkening and the fourth and fifth very dark, like the legs; claws simple. Abdomen dark grayish brown, lacking distinct annulations. The tenth tergum is strongly sclerotized, its surface glossy. Cerci narrowed in apical one-third and darkened at their tips (Fig. 136); the hypovalves taper rather evenly to a slender tip, instead of being truncate with a projecting apical tooth as in *americana*. Body length of holotype female 15.0 mm.; wing 12.9 mm.

Type.—Holotype female; about 30 miles north of Seward, Kenai Peninsula, Alaska (60°31′N, 149°32′W), 30 June 1957, George W. Byers (Field Catalogue Number 22); in the Snow Entomological Museum, University of Kansas, Lawrence, Kansas.

Descriptive comments.—It is anticipated that discovery of the male of this species will provide additional characters to separate it from *Dolichopeza americana*. At present, the larger size of *borealis*, its peculiar tarsal coloration (which is presumed to be the same in both sexes), and details of structure of the ovipositor will serve to distinguish the two species.

The tarsi in *borealis* are proportionately shorter than in most species of the genus. Thus, while the tarsi of *americana* exceed the combined lengths of femur and tibia, those of *borealis* (assuming the type is representative) are noticeably shorter, as shown in Table 4.

TABLE 4.—Measurements of Leg Segments in *Dolichopeza* (*D.*) *borealis* (Measurements in Millimeters)

	Femur	Tibia	Tarsus	(Basitarsus)	Total
Fore leg	6.1	6.0	9.9	(7.2)	22.0
Middle leg	6.6	6.8	9.7	(6.7)	23.1
Hind leg	7.1	7.0	10.0	(7.1)	24.1

Geographical distribution.—*Dolichopeza* (*D.*) *borealis* is so far known only from the type locality on the Kenai Peninsula, and it seems likely that its range does not extend far northward or eastward from there. It may, however, occur in the forested lowlands of southwestern Alaska and, if the shade provided by trees is not a limiting factor in its distribution, in the Aleutian Islands.

Habitats.—The holotype was taken in fairly deep shade at the edge of a clump of spruce trees in a hummocky bog, in which species of *Sphagnum* were the predominant mosses. There was much fallen timber in the bog and a widespread undergrowth of brushy, moose-browsed willow. In the open areas among the willows, grasses, sedges and wild rose were growing in the mosses, and there were scattered, small areas of open water.

Seasonal distribution.—The collection date in late June makes it difficult to say whether there are one or two annual generations, but on the basis of knowledge of the other species of the genus it seems reasonable to expect only one summer generation at the latitude of the type locality.

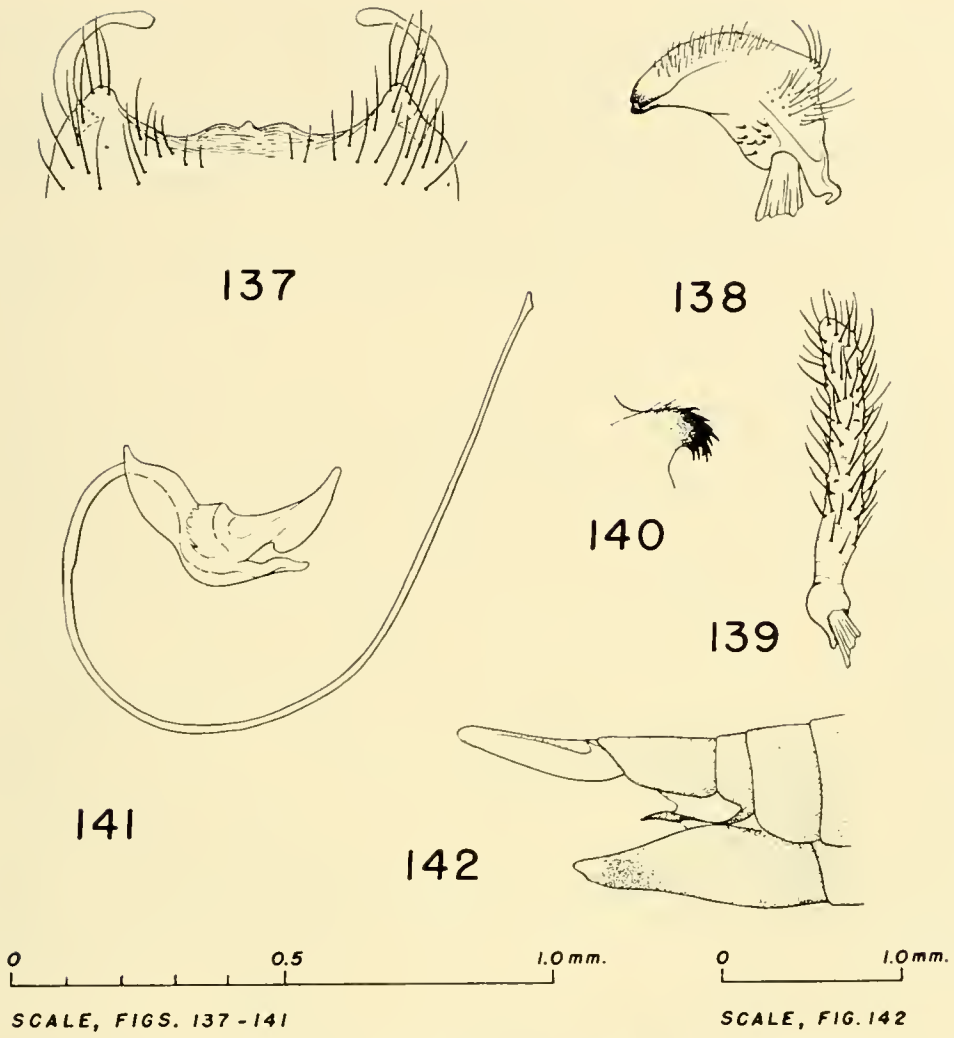
Immature stages.—None of the immature stages of this species is so far known.

Subgenus *Oropeza*

Dolichopeza (*Oropeza*) *australis*, new species

Among specimens of *Dolichopeza subalbipes* from various localities on the southeastern coastal plain, I have found several flies resembling that species in some respects but differing in details of coloration and structure. The following description is based upon 22 males and eight females from Georgia (type series) and two males and two females from other areas. The specific name refers to the fact that this species has the southernmost over-all range of any North American *Dolichopeza.*

Description.—General body coloration light brown with dark brown markings, the tarsi pale. Prescutum dark brown, a pattern of three dark stripes sometimes faintly indicated but usually obscured altogether. (There is, in some specimens, a slightly paler



FIGS. 137-142. *Dolichopeza (Oropeza) australis* new species; 137—ninth tergum of male, 138—left inner dististyle of male, dorsal aspect, 139—left outer dististyle, dorsal aspect, 140—gonapophysis, dorsal aspect, 141—vesica and penis, 142—terminal abdominal segments of female, right lateral aspect.

median line, but I believe this is a post-mortem effect.) Mesothoracic anepisternum brownish, only a little darker than adjacent portion of pre-episternum. Eyes black. Antennae with twelve segments, the scape and pedicel slightly paler than the dusky flagellum. Wings tinged lightly with brown, the stigma darker brown. Femora and tibiae brown, this color extending over approximately the basal two-thirds of each basitarsus and grading through yellowish brown to pale yellowish white on the second through fifth segments. Abdomen light brown with distinct darker brown annulations. The medio-posterior margin of the ninth tergum of the male has a central, pointed tooth with a broader, rounded lobe on either side, the central tooth the longest; and the tergal arms are slender, their tips flattened and slightly widened (Fig. 137). Gonapophyses

set with black bristles, as in other species of the *obscura* group. Inner dististyles with an angular protuberance on the outer surface, the elevated area bearing a few strong hairs (Fig. 138). Hypovalves of female ovipositor moderately darkened subapically (Fig. 142). Body length of males is 8.0 mm. to 9.8 mm. (holotype 9.5 mm.); of females 9.8 mm. to 11.6 mm. (allotype 9.8 mm.). Wing length in males varies from 10.4 mm. to 11.8 mm. (holotype 10.9 mm.); in females, from 10.2 mm. to 12.8 mm. (allotype 10.6 mm.).

Types.—Holotype male, Mossy Pond (Emory University Field Station, near Newton), Baker County, Georgia, 27 January 1949, R. E. Bellamy (Catalogue Number 2936). Allotype, same locality and collector, 31 March 1949 (Catalogue Number 3007). Paratypes, 21 males and 7 females from the type locality, as follows: 27 August 1948, 1 ♂ ; 27 January 1949, 1 ♀ , taken in copulation with the holotype but too damaged to be made the allotype; 9 February 1949, 1 ♂ ; 17 February 1949, 1 ♂ , 1 ♀ ; 24 February 1949, 1 ♂ ; 24 March 1949, 7 ♂ , 4 ♀ ; 31 March 1949, 6 ♂ , 1 ♀ ; 7 April 1949, 1 ♂ , 1 ♀ ; 21 April 1949, 3 ♂ ; all collected by Dr. R. E. Bellamy. Holotype, allotype and most of the paratypes are in the University of Michigan Museum of Zoology, Ann Arbor, Michigan; one male paratype has been sent to the United States National Museum, Washington. The few specimens seen from areas other than the type locality have not been designated paratypes.

Descriptive comments.—Dolichopeza australis is most nearly related to *subalbipes* and *johnsonella,* as indicated by the hypopygial structure of the male, especially the inner dististyles and the posterior margin of the ninth tergum. In body coloration, *australis* resembles *johnsonella,* the thoracic pleura lacking the contrast in shade and color along the border between anepisternum and pre-episternum, as found in *subalbipes,* and the prescutum being obscurely marked. However, the coloration of the legs and details of the external reproductive structures of both sexes will easily separate the two species. In *subalbipes,* the tarsi are white and the femora and tibiae are pale with darkened tips, and a part of the last tarsal segment is darker than the remainder of the tarsus. In contrast, the leg segments of *australis* are neither pale nor dark tipped, and the tarsi are pale throughout. The characteristic basal enlargement of the penis in *subalbipes* is only faintly indicated in *australis* (Fig. 141), and details of the external genitalia as well will serve to distinguish these two species. Certain male flies assigned to *subal-*

bipes have slender tergal arms similar to those of *australis*, but the two species may be differentiated by the shape of the margin of the ninth tergum and by the color differences already mentioned.

Of the type series of flies, about one quarter have venational abnormalities in one or both wings. Most of these anomalies consist of absence of a closed cell 1st M_2 (discal cell) by loss of the medial cross-vein.

Geographical distribution.—Dolichopeza australis is so far known from only three localities, one of which is the type locality in southwestern Georgia. The other two, Washington County in southwestern Alabama and Alachua County in northern peninsular Florida, suggest a rather widespread occurrence of the species on the Gulf Coastal Plain. Habitats similar to those in which *australis* has been found also occur in southern Mississippi and Louisiana.

Habitats.—All known habitats of this species are swamps—that is, wooded areas with lush undergrowth and considerable amounts of standing water. Mossy Pond, the type locality, is an isolated cypress swamp of a few acres extent, surrounded by rather dry land that is sparsely wooded with pines. The cypresses are festooned with Spanish moss, while the water below supports a luxuriant growth of floating and emergent vegetation. Mosses growing above the water line on the cypress boles and at the edge of the pond are probably the larval habitat of *australis* and of the other species of *Dolichopeza* (*obscura* and *subalbipes*) found together with it.

Seasonal distribution.—It has been mentioned earlier that in the southernmost part of the range of the genus in North America, *Dolichopeza* seems to reproduce and complete its life cycle as rapidly as local conditions will permit; that is, there is no limitation to one or two annual generations. Date records for *australis* include January, February, March, April and August at the type locality, with the largest numbers having been taken in the last half of March. Records from Alachua County, Florida, are for 12 and 14 November and 16 January, and from Washington County, Alabama, 14 June.

Immature stages.—Eggs of this species average .71 mm. in length and .31 mm. in greatest diameter. They do not have a terminal filament. Larvae and pupae of *australis* have not yet been found, as I have never had the opportunity to study this species in the field. During my brief visit to the type locality, in April, only *Dolichopeza obscura* was collected, and I have never seen even the adults of *australis* alive.

Dolichopeza (*Oropeza*) *carolus* Alexander

Literature references.—*Oropeza albipes* Johnson. Johnson, 1909: 121, pl. 15 (hypopygium); Johnson, 1910: 708; Alexander, 1919: 930; Alexander and McAtee, 1920: 393; Dietz, 1921: 259; Alexander, 1924: 60; Alexander, 1925: 172; Johnson, 1925: 32; Pierre, 1926: 11; Leonard, 1928: 698; Alexander, 1929a: 236; Alexander, 1929c: 297; Alexander, 1930c: 113; Rogers, 1930: 22; Rogers, 1933: 48.

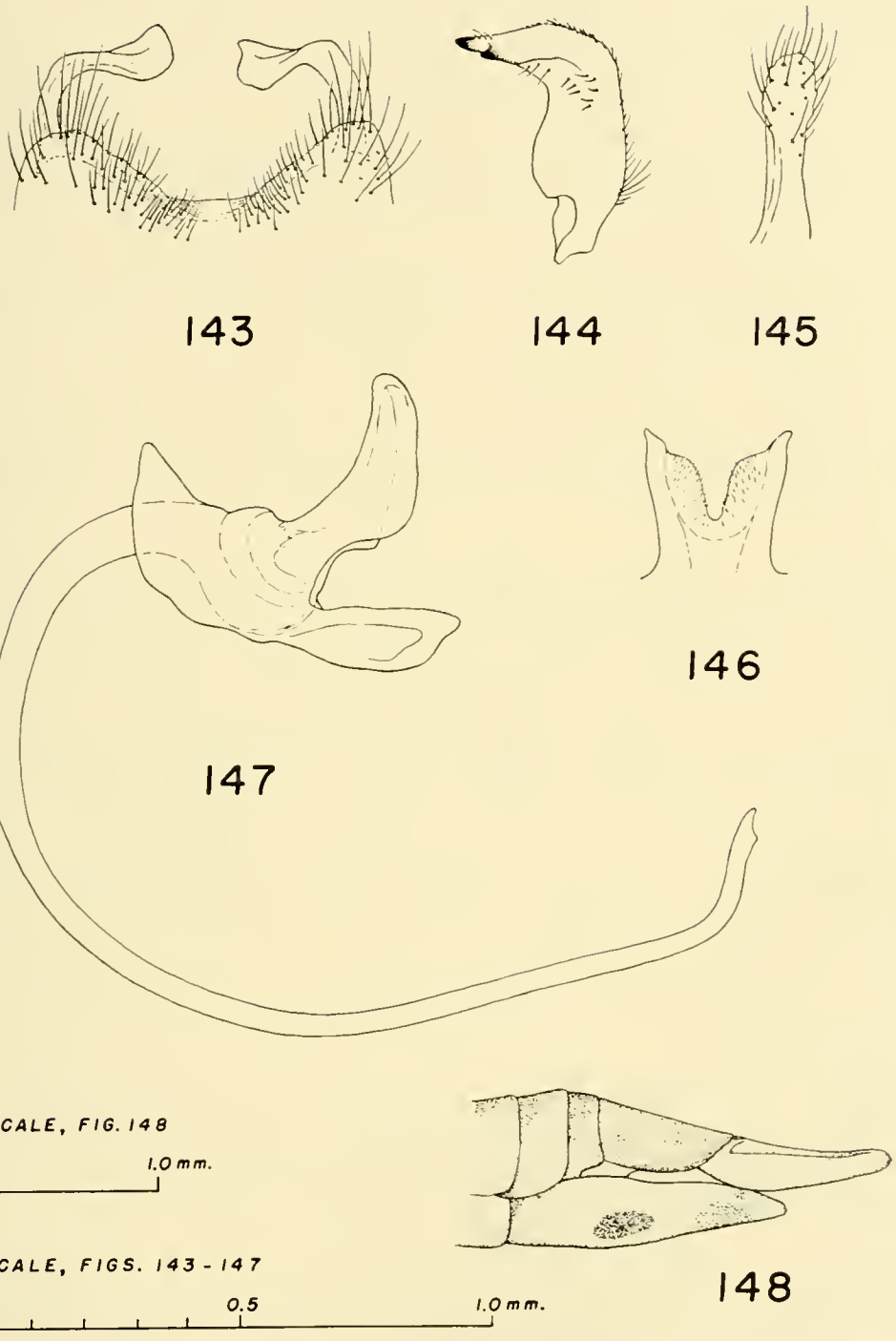
Dolichopeza (*Oropeza*) *carolus* Alexander, new name for *Oropeza albipes* Johnson, preoccupied in *Dolichopeza* by *D. albipes* (Ström). Alexander, 1940: 618; Alexander, 1941a: 295; Alexander, 1942: 211-212, fig. 26A (hypopygium); Whittaker, 1952: 32; Foote, 1956: 221.

Original description.—"Face yellow, rostrum and vertex brown, palpi brown. Antennae yellow, the three basal joints lighter than the others. Thorax dark brown, showing three rather distinct stripes; plurae, scutellum, and metanotum light yellow, translucent, with livid spots below the base of the wings, between the coxae, at the base of the halteres, and on the posterior margin of the metanotum. Abdomen yellow, the black bands connected on the dorsal line leaving a row of large spots on the sides as in *O. venosa.* In the female the bands are more distinct. Genitalia yellow, appendages light yellow, very short or rudimentary, style red, base black, appendages at base of style short and tipped with a slightly curved spine, ventral margin deeply emarginate. Ovipositor reddish brown. Femora yellow, tibiae and tarsi white, tipped with brown. Halteres white, knobs brown. Wings brownish hyaline, veins light brown, stigma dark brown, median cubital cross-vein * present or wanting. Length, male, 10 mm.; female, 13 mm."

Types.—Holotype male, Cohasset (Norfolk County), Massachusetts, 1 July 1907, Owen Bryant. Allotype, Dummerston (Windham County), Vermont, 14 July 1908, C. W. Johnson. Paratypes, six males and four females, together with holotype and allotype in the collection of the Museum of Comparative Zoology, Harvard University; one male and one female in the Academy of Natural Sciences of Philadelphia; and one male in the Alexander collection, at Amherst, Massachusetts. Johnson mentions having twenty-two specimens; however, it is possible that he did not make types of all of them.

Diagnostic characteristics.—Among the species of *Oropeza* in North America, only two possess white tarsi and pale legs, with the tips of femora and tibiae darkened. These are *carolus* and

* See page 710.



FIGS. 143-148. *Dolichopeza (Oropeza) carolus;* 143—ninth tergum of male, 144—left inner dististyle of male, dorsal aspect, 145—left outer dististyle, dorsal aspect, 146—gonapophyses, dorsal aspect, 147—vesica and penis, 148—terminal abdominal segments of female, left lateral aspect.

subalbipes. The similarity of coloration and size in these two species is striking, involving nearly every detail. In the field, habitat is an indication of species identity, *carolus* being more often found in rocky places and moist to mesic forests and *subalbipes* in wetter woodlands, along stream banks, and in swamps and marshes. Males of *carolus* may be identified with certainty by their short, pale outer dististyles. Females may be separated from those of *subalbipes* by the presence of a dark, well-defined spot on the basal portion of the hypovalve, on each side, approximately below the ninth tergum (Fig. 148). The absence of sharp contrast of color between the mesothoracic anepisternum and preepisternum in *carolus* is also an aid in distinguishing this species from *subalbipes*. All these features are visible to the unaided eye, so that field determination of collected specimens is not difficult.

Descriptive comments.—The similarity of coloration between *carolus* and *subalbipes* extends to virtually every feature except those few enumerated above, but the darker markings are more intense in *subalbipes*, in specimens that are not faded with age. While *carolus* is a fly of contrasting colors, these are, as in all of the genus, usually more subtle than the paint-box assortment indicated in Johnson's description. There is a degree of brown in all the colors, so that in general appearance *carolus* is light tawny with dark brown markings. Against a dark background, the tarsi are pale enough to be called white, without any chance of confusion. Old or sun-faded specimens take on the appearance of *Dolichopeza venosa*, which species is easily recognized in both sexes by the genitalia.

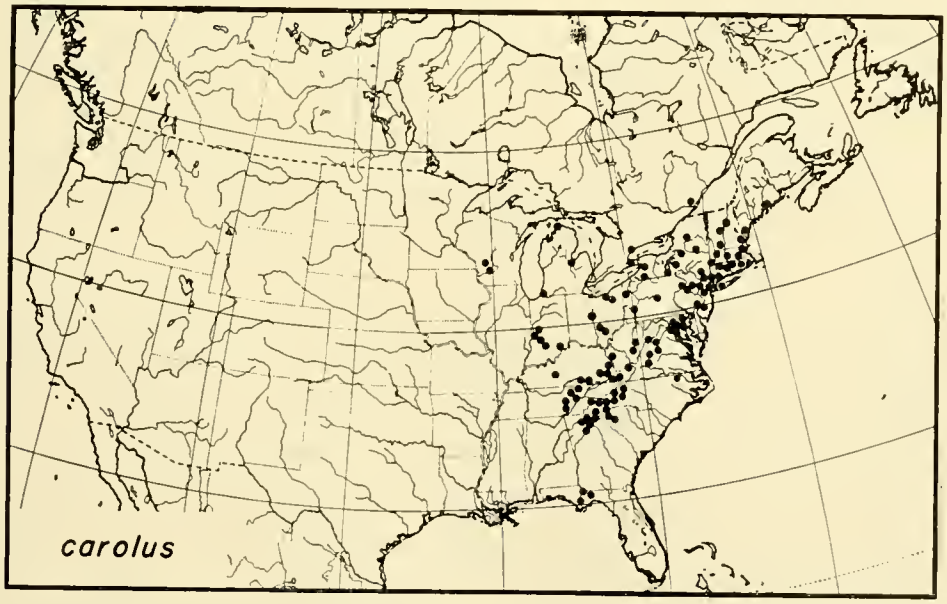
Wing venation in *carolus* deviates only rarely from the subgeneric scheme. An occasional absence of the medial cross-vein or failure of some branch of the media to reach the wing margin are the most commonly seen anomalies. In a collection of 40 males and 20 females from a Georgia locality, only four venational abnormalities were found: one incompletely closed discal cell and three instances of a short spur vein projecting distally from the medial cross-vein. The latter anomaly has also been seen from a few other localities.

Body length of males is from slightly less than 10 mm. to somewhat over 12 mm.; and the wings vary within the same limits. Females measure about 11 to 15 mm., their wings from 10 to 14 mm. The smaller specimens are from August collections, and the larger ones are spring records from Indiana, Michigan and mountainous western Virginia.

Variation in details of the male hypopygium is slight and is found mostly in the shapes of the ends of the tergal arms and of the inner dististyles. The widened, flattened tips of the tergal arms may be elongate, rounded or somewhat pointed, and it is often the case that the two arms of the same fly are unlike (Fig. 143). Curvature of the inner dististyles varies, as does the depth of the apical cleft. It should be mentioned that the apparent shape of such flattened or partially flattened structures as the tergal arms and (in this species) the outer dististyles is considerably affected by a shift in the point of view. Thus, in dorsal aspect (Fig. 145) the outer dististyle seems somewhat narrowed in the basal half, while viewed from the side it is of almost equal width throughout. In the emargination of the ninth tergum and the shape of the tergal arms, *carolus* most nearly resembles *walleyi* and *sayi,* but the gonapophyses are rather like those of *dorsalis.*

The size and configuration of the vesica and its apodemes and the diameter and apical curvature of the penis suggest a relationship of this species with *Dolichopeza venosa* (compare Figs. 147 and 234). The seminal duct in *carolus* is only about one-third as long as that of *polita,* a species of comparable size, and the bases of the accessory glands are enlarged, resembling the common vas deferens at the point where all three ducts enter the seminal vesicle.

Geographical distribution.—The known range of *Dolichopeza carolus* extends from Maine westward to Wisconsin and southward through the Appalachian Mountains. Following cool ravines along



MAP 2. Range of *Dolichopeza (Oropeza) carolus* Alexander. Each spot represents one or more collections within a county (United States) or at a locality.

the Chattahoochee-Apalachicola drainage, *carolus*, apparently an essentially northern species, has reached western Florida, where it is a common member of the tipulid fauna of the Apalachicola River valley, an area unlike the rest of the state. I did not find in the Ozark Mountains what I consider adequate *carolus* habitats, but I would expect to find this species in parts of Minnesota, western Ontario, and other northern areas from which it is not known at this time. There is a published record of the occurrence of this species in New Brunswick (Alexander, 1942: 211), but I have not been able to get more specific data, for which reason the record does not appear on the map.

Habitats.—Adults of *Dolichopeza carolus* are most commonly taken in leafy vegetation, such as is found along small streams through deciduous forests or in rocky ravines where leafy plants and ferns abound. I have never found them far from water or cool shade, although by night or on damp days they may fly a hundred yards or so from their usual streamside haunts. They are numerous in Michigan woodlands in low vegetation in the wetter areas. I found them particularly abundant in the sandstone ravines of Indiana and Ohio, where they rested among ferns and other low plants along the edges of outcropping strata or suspended themselves in the deeper shade of a cranny beneath an outcrop. Following small brooks upstream, I encountered *carolus* nearly as far as there were trees providing shade. Dietz (1921) records *carolus* as ". . . common, June and July, in damp, open woods." On the Cumberland Plateau, Rogers (1930) found them ". . . equally characteristic of wet 'rock-houses,' of the shaded base of dripping cliffs, of upland stream-margin thickets, and of the mossy banks of shaded brooks." In the Florida area mentioned earlier, *carolus* was found in ". . . moist recesses beneath overhanging banks and within rank herbage on shaded stream banks" (Rogers, 1933). Foote (1956) records the species from moist woodland ravines and wet cliff faces.

I have taken *carolus* together with *subalbipes* in deep grasses and broad-leafed weeds along a stream in Virginia, among ferns along a mountain brook in Maine and in a swamp in Wisconsin. In the brushy margin of a mountain bog in Pennsylvania, I took it together with *venosa*, while along a rocky brook course a mile down the mountain it was found together with *americana*. It is my belief that the species does not range far from its larval habitats, which are wet or damp mosses usually occurring near small streams. On one occasion, however, several teneral flies were captured on

a mossy but not wet cliff face at 6:30 in the evening, but when I returned to the same spot an hour after nightfall, these and many other adults seen earlier were nowhere to be found.

Seasonal distribution.—From southern Michigan and New England to Georgia, *carolus* seems to have two main periods of emergence annually: one in late May and June, the other in late July through August, the period in any case governed in part by the local weather conditions. Nearly all western Florida records are for March and April, although later summer months are represented. In Michigan and in Wisconsin, *carolus* is on the wing throughout July but mostly early in the month. In Turkey Run State Park, Parke County, Indiana, in 1953, the first individuals of *carolus* were observed on 1 June, two weeks after the start of the emergence of *americana* and nine days after *polita* first appeared. Only a few females were found as late as 10 July, although one mating pair was collected on 12 July. In Neel Gap, Union County, Georgia, in 1952, *carolus* had reached peak emergence on 28 June. Six years later, at the same place, equivalent numbers were found on 10 June.

Immature stages.—Eggs of this species are comparatively wide for their length, measuring around .79 mm. long and .37 mm. wide. Not many more than a hundred eggs appear to be matured and laid by one female. Eggs laid on 15 June, in Indiana, hatched nine days later at outdoor temperatures. In connection with oviposition, there is an interesting observation to relate: while all other species of *Dolichopeza* induced to lay eggs in captivity laid them on or near wet paper pads in the bottoms of the breeding jars, all females of *carolus* (several individuals, in two years) deposited their eggs upon the sides of the glass jars, as if avoiding the paper. Now, if the tip of the ovipositor is sensitive to the appropriate larval environment (see account of oviposition), then this peculiar behavior may have some bearing on the kind of habitat in which the eggs are laid under natural conditions.

The first instar larvae cannot be distinguished from those of other species, at this time, and I have not succeeded in rearing them to the later instars or in locating the latter in their natural habitats. I would expect the larvae of *carolus* to resemble rather closely those of *subalbipes* and *venosa*. Not until the summer of 1958 was I able to find pupae of this species, and I hasten to add that these have been identified only by inference, on the basis of comparison with known pupae and by close association with adult flies. At a Penn-

sylvania locality, in a season when adults of *americana* and *carolus* only were present, both male and female pupal skins of a species of *Oropeza* were found projecting from mats of the mosses *Tetraphis pellucida* and *Leucobryum glaucum*. The mosses were growing on root-bound soil on the bank of a small brook below a spring. Beneath wood ferns and low broad-leafed plants only a few inches from the pupal site, adults of *carolus* were resting. The pupae most nearly resembled those of *subalbipes* but appeared to belong to a species of the *sayi* group—a combination one would almost expect on the basis of the adults. Their size, the configuration of their spiracular yokes, and other characters (see key to pupae, page 773) make it virtually certain that these are the pupae of *carolus*.

Notes on distribution.—CONNECTICUT—Fairfield County, 23 August; Hartford County, 8 June and 9 July; Litchfield County, 9 July and 23 July to 12 September; Windham County, 30 June. FLORIDA—Gadsden County, 19 April; Leon County, 16 March to 25 May; Liberty County, 27 March to 26 April and 15 to 27 July. GEORGIA—Dawson County, 9 to 27 June; Hall County, 6 June; Lumpkin County, 8 June; Rabun County, 20 May to 12 June and 20 August; Union County, 10 and 28 June. INDIANA—Jefferson County, 3 June and 23 August; Monroe County, 23 June; Montgomery County, 28 June; Owen County, 18 to 27 June; Parke County, 9 June to 15 July and 30 August. KENTUCKY—Bell County, 18-19 June; Edmonson County, June (?); Letcher County, 3 July; Pike County, 3 July; Whitley County, 24 June. MAINE—Hancock County, July; York County, 1 July. MARYLAND—Baltimore County, 17 June; District of Columbia, 30 May and 25 August; Montgomery County, 4 to 15 June, July, and 29 August to 5 September; Prince George's County, 29 June. MASSACHUSETTS—Berkshire County, 12 to 30 June; Hampshire County, 14 July and 9 August; Middlesex County, 7 June; Norfolk County, 1 and 10 July. MICHIGAN—Berrien County, 8 to 17 July; Cheboygan County, July; Saginaw County, 6 June. NEW HAMPSHIRE—Grafton County, 4 July; Rockingham County, no date. NEW JERSEY—Bergen County, 21 June; Burlington County, 3 to 11 August; Morris County, 17 June; Warren County, 11 July. NEW YORK—Cattaraugus County, 4 July; Columbia County, mid-August; Cortland County, 20 July; Erie County, 3 to 10 July; Fulton County, 28 June; Herkimer County, 20 June; Oneida County, July; Orange County, 25 June to 28 July and 27-28 August; Suffolk County, 25 June and 9 August; Tompkins County, 14 July; Ulster County, 28 June; Westchester County, 9 June. NORTH CAROLINA—

Avery County, 14 June; Buncombe County, 15 June; Burke County, 14 June and 9 July; Haywood County, 27 July to 2 August; Macon County, 8 to 22 June; McDowell County, 13 June; Northhampton County, 7 June; Transylvania County, 9-10 June; Yancey County, 10-11 and 22 June. OHIO—Cuyahoga County, 24 June; Delaware County, June; Fairfield County, 8 June; Hocking County, 30 May and 6 to 8 June; Portage County, 24-25 June and 14 July. ONTARIO—Jordan (near Niagara Falls), 1 August; Toronto, 4 July. PENNSYLVANIA—Allegheny County, 14 June; Carbon County, 3 July; Centre County, 13 and 25 June, 2 to 9 July and 5 August; Luzerne County, 13 to 27 June and 5 to 24 July; Mercer County, 25 June; Monroe County, 6 August; Philadelphia County, 31 July, 2 August and 2 September. QUEBEC—Montreal, June. RHODE ISLAND—Kent County, 21 June. SOUTH CAROLINA—Greenville County, 7 June and 1 September; Pickens County, 29 June. TENNESSEE—Bledsoe County, 26 June; Cumberland County, 25 June; Fentress County, 6 June to 16 July and 16 August; Morgan County, 12 June and 5 August; Scott County, 28 to 30 May; Sevier County 10 to 12 and 30 June. VERMONT—Orange County, 11 July; Windham County, 14-15 July. VIRGINIA—Arlington County, 6 June to 4 July and 11 to 25 August; Augusta County, 28 June; Bedford County (locality uncertain), 30 June; Fairfax County, 29 May to 9 June, 11 to 25 July, and 22 August to 5 September; Giles County, 3 June to 13 July and 24 July to 29 August; Rockingham County, 6 July; Shenandoah National Park, 6 July; Smyth County, 20 June; Washington County, 2 July; Wise County, 2 July. WEST VIRGINIA—Mingo County, 3 July; Pendleton County, 26 June; Pocahontas County, 5 July and 7 August; Randolph County, 5 July. WISCONSIN—Juneau County, 6 July; Sauk County, 5 July.

Dolichopeza (*Oropeza*) *dorsalis* (Johnson)

Literature references.—Oropeza dorsalis Johnson. Johnson, 1909: 119-120, pl. 15 (hypopygium); Alexander, 1919: 930; Alexander and McAtee, 1920: 393 (possibly misidentified); Johnson, 1925: 33; Pierre, 1926: 11; Alexander, 1928: 57, Alexander, 1931a: 138.

Oropeza rogersi Alexander. Alexander, 1922a: 6-7; Pierre, 1926: 12.

Oropeza dorsalis rogersi Alexander. Rogers, 1933: 49.

Dolichopeza (*Oropeza*) *dorsalis* (Johnson). Alexander, 1941a: 295; Alexander, 1942: 212, fig. 26B (hypopygium); Rogers, 1942: 59.

Dolichopeza (*Oropeza*) *sessilis* Alexander. Alexander, 1941a: 296-297, fig. 1 (wing) (new synonymy).

Dolichopeza (*Oropeza*) *dorsalis rogersi* (Alexander). Alexander, 1942: 212 (new synonymy).

Original description.—"Face yellow, rostrum and vertex dark brown, palpi blackish; antennae with three basal joints yellow, the remainder fuscous. Thorax dark brown, the three stripes indistinct, the brown extending over the scutellum and metanotum as a broad stripe, leaving only a narrow lateral margin of yellow; pleurae yellowish white, subtranslucent. Abdomen yellow with a dorsal stripe of brown, spreading over the third to the seventh segments and somewhat obscuring the black bands. Genitalia yellowish, appendages black, style short, ventral margin deeply emarginate. Ovipositor brown. Halteres yellow, knobs dark brown. Legs brown, coxae and basal portion of the femora yellow. Wings light smoky brown, veins and stigma slightly darker, the petiole between the discal and second posterior cell very short, the median cubital cross-vein* present. Length, male, 9 mm.; female, 10.5 mm."

Types.—Holotype male, Capens (on Deer Island, Moosehead Lake, Piscataquis County), Maine, 14 July 1907, C. W. Johnson. Allotype, same locality and collector, 15 July 1907. Both are in the collection of the Museum of Comparative Zoology at Harvard University.

Diagnostic characteristics.—The contrasting dark dorsum and pale sides and underparts of the thorax of *dorsalis* make it readily identifiable on sight, both in the field and laboratory, sight recognition being easier, however, when the fly is alive, the contrast then seeming greater. In its natural habitat, this species is most likely to be confused with *Dolichopeza walleyi* or *sayi*, which often occur together with it. From *sayi*, it differs in details of the external reproductive structures in both sexes and in coloration, especially of the thoracic pleura, pale in *dorsalis* and darkly colored on the anepisternum and ventral pre-episternum in *sayi*. Preserved specimens closely resemble the form of *walleyi* that has pale thoracic pleura, particularly if the prescutal stripes are at all distinct. Males of these two species are easily differentiated by hypopygial characters. The faintness of abdominal annulations and the shorter, more heavily sclerotized cerci of females of *dorsalis* will aid in distinguishing them from *walleyi* females having pale pleura, generally yellowish coloration, and the stigmal spot of the wing not deeply colored. Also, the knobs of the halteres are very dark gray-brown in *dorsalis* but are only slightly infuscated in *walleyi*.

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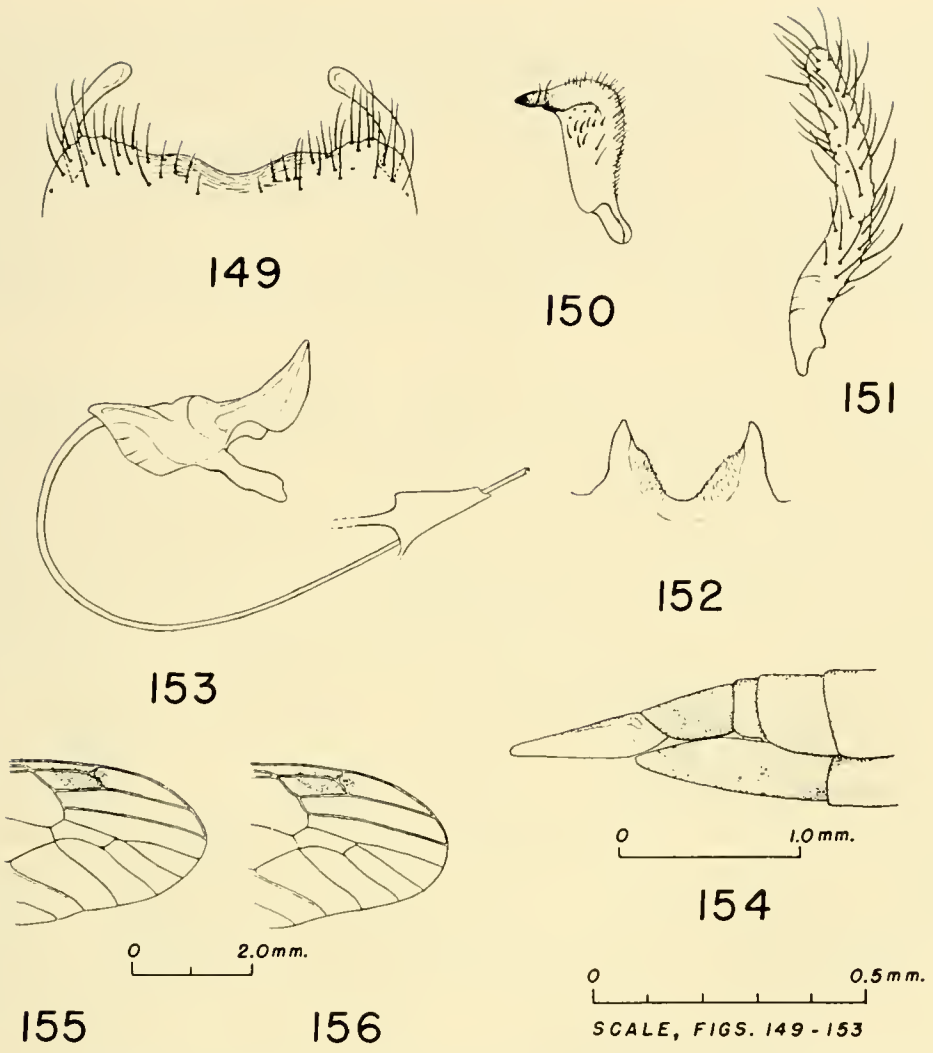
* See page 710.



FIGS. 149-156. *Dolichopeza (Oropeza) dorsalis;* 149—ninth tergum of male, 150—left inner dististyle of male, dorsal aspect, 151—left outer dististyle, dorsal aspect, 152—gonapophyses, dorsal aspect, 153—vesica, penis and adminiculum, left lateral aspect, 154—terminal abdominal segments of female, right lateral aspect, 155—apex of wing, showing cell M_1 with short petiole, 156—apex of wing showing sessile cell M_1.

Descriptive comments.—Dolichopeza dorsalis is a small, tawny-yellow fly with a dark, brownish thoracic dorsum and with amber-tinged wings that are relatively wider for their length than in other North American species of the genus. The coloration of the dorsal sclerites of the thorax varies from a rich cinnamon brown to very dark brown. Females, and less often males, may not have the dark coloration extending uninterruptedly along the abdominal terga, as described by Johnson.

An outstanding and very common variation in wing venation in this species is the shortening of that part of the vein M_{1+2} which forms the petiole of cell M_1, that cell being correspondingly elon-

gated. This is mentioned by Johnson in the original description and again in the description of *Oropeza rogersi* (Alexander, 1922a: 6). In every large sample of a population of *dorsalis*, I have found a few flies in which this petiole was extremely short (as Fig. 155) or absent completely (as Fig. 156). In fact, several individuals have been seen in which the cell M_1 was petiolate in one wing and sessile in the other! In view of this, I have placed *Dolichopeza* (*Oropeza*) *sessilis*, distinguished from *dorsalis* by having the cells M_1 sessile, in synonymy with *D.* (*O.*) *dorsalis*.

Dolichopeza dorsalis is the smallest North American representative of the genus, although some males of *americana* and very rarely of other species will be smaller than the average *dorsalis*. Males range in length from about 7 to 10 mm., most being close to 9 mm. Their wings vary from 8.5 to 11 mm. and usually slightly exceed the length of the body. Females measure 9.5 to 12 mm. in body length and 9 to 11 mm. in length of wing. Throughout the range of the species, quite small individuals may be found. On the basis of certain of these, Alexander (1922a: 6) described *Oropeza rogersi*, which was stated to differ from *dorsalis* only in size. In a later review of the genus, Alexander (1942: 212) regarded this small form as a subspecies of *dorsalis*, having a range from southern Indiana eastward to Virginia and southward to Florida. Rogers, nine years earlier, had also considered *rogersi* a subspecies of *dorsalis* (Rogers, 1933: 49). However, among the specimens available to me there are individuals from Michigan and British Columbia that are of small enough size to fit the description of the southern race, *rogersi*, while many specimens from within the described range of *rogersi*, including some from the type locality, are as large as any northern *dorsalis*. Because of this situation, I consider *Dolichopeza* (*Oropeza*) *dorsalis rogersi* a synonym of *dorsalis*.

In its general profile, the ninth tergum of the male of *dorsalis* suggests that of *johnsonella*, although the lateral shoulders are less prominent and the tergal arms are proportionately shorter and more rounded at the tips (Fig. 149). The inner dististyles (Fig. 150) are more like those of *walleyi* or *sayi*, while the gonapophyses most nearly resemble those of *carolus* (Fig. 152). The edge of the gonapophysis that bears the smooth, spinous tip may be dorsolateral in position or may be slightly rotated into a dorsal position. The outer dististyles are very dark brown, except at their bases, which are pale like the rest of the hypopygium. The adminiculum is short, conical and strongly sclerotized.

Except for the venational variation already mentioned, the wings show few departures from the subgeneric pattern. A small closed cell at the distal end of the discal cell connecting it with the cell M_1 has been seen once.

Dolichopeza dorsalis rests with wings outspread and tilted slightly forward. I have noticed that this species sometimes, instead of hanging from overhead support, stands upon vegetation, especially the bent-over leaves of grass. It is a very alert fly, which takes to the wing at the slightest alarm.

Geographical distribution.—Dolichopeza dorsalis is the second most widespread member of its genus in the world. Apparently without subspeciation, it ranges across three thousand miles of

MAP 3. Range of *Dolichopeza (Oropeza) dorsalis* (Johnson). Each spot represents one or more collections within a county (United States) or at a locality.

North America, from Florida and New England northwestward to the Yukon. Its distribution within this vast area (see map) is very poorly known, and extensive further collecting is necessary, especially in the provinces of Canada and the middle Atlantic states, to bridge existing gaps in the range. Only recently (summer of 1959) this species was discovered in an apparently isolated habi-

tat in the Black Hills of southwestern South Dakota. Its occurrence there is discussed more fully in the conclusions.

Habitats.—This species is usually found associated with bogs, swamps and brushy marsh borders. In Michigan, *dorsalis* is "common in shrub and shrub-sedge marshes and near the shrub bordered margins of the sedge-fern-grass marshes. Numerous but local . . . in a variety of other shaded wet situations: tamarack-sumac swamps, birch-maple swamps, and shaded seepage areas" (Rogers, 1942: 59). The holotype of *Dolichopeza sessilis* was collected ". . . in a small accessory swampy patch just off the main stream. . . ." at 2200 feet elevation, in the Great Smoky Mountains, North Carolina (Alexander, 1941a: 296). Rogers (1933: 49) reports *dorsalis* collected in "rank herbage of swampy or marshy rills," in Jackson and Liberty counties, western Florida. The South Dakota habitat was a marsh of grasses, *Carex* spp., *Osmunda* fern, low willow brush, etc., below a spring—a habitat similar in many details to places in which I have collected *dorsalis* in Michigan, Minnesota and elsewhere. *Dolichopeza sayi* often occurs together with *dorsalis* in such environments, but in the Black Hills that species was replaced by the dark form of *walleyi*.

Seasonal distribution.—There is evidence of two annual generations in the collection records from southern Michigan, southern Indiana and North Carolina. Most of the Florida specimens were taken in April, and all were collected in spring. Further north, the first emergence is in June and the second in August. Rogers (1942: 59) estimated the emergence periods, in Livingston County, Michigan, to be from 4 June to 14 July and from 11 to 30 August, in the years 1936 through 1938. The records for farther north in Michigan and for Minnesota, Ontario, and Manitoba, as well as for South Dakota, are all very late June or July. In these regions, it is probable that there is but one generation per year. It is not clear from the collection records in Alberta and northern British Columbia whether there are one or two generations per year in those areas. The latitude would lead me to expect but one; however, at Liard Hot Springs, northern British Columbia, on 13 June 1957, while enroute to Alaska, I found only males of *dorsalis,* suggesting that the flight period was just beginning. Returning on 8 July, I found only females. If the period of emergence of adults had progressed as rapidly as indicated by these collections, it is possible that a second generation might have been produced before the onset of freezing weather.

Immature stages.—The eggs of *dorsalis* average .76 by .31 mm., which is rather large, considering the size of the adult female. I have no counts of the quantity laid by one female but would estimate the number to be ninety. Larvae began to hatch on 22 July from eggs that had been laid on 12 July, by females taken at Lake Itasca, Clearwater County, Minnesota. The first instar larvae of *dorsalis* are of a more buffy color than are those of the other species.

Larvae of *dorsalis* are bright greenish, like the background color of *americana* larvae. Since the green color is not partly concealed by transverse ridges of microscopic hairs on most of the dorsum, as it is in some other species, the larva has by comparison a rather striking appearance. The greenish color is dulled, however, in the thoracic and eighth abdominal segments, by the presence of microscopic hairs that are so long and dense that they give a "woolly" appearance at high magnifications.

The color of the body of the larva probably results from and changes according to the foods chosen by the larva. To see whether this is the case, I offered leaves of *Sphagnum rubellum*, which are dull red in color, to a larva that had been feeding on a green species of *Sphagnum*, probably *S. palustre*. During the several weeks that both mosses were offered as food, however, the larva never fed on the red moss. *Dolichopeza dorsalis* is the only species the larva of which is known to feed on *Sphagnum*, but it is not limited to that genus, having been taken also in *Amblystegium varium*, and possibly in *Plagiothecium denticulatum* growing together with the *Amblystegium* on the floor of a marsh. From these same mosses were reared *Tipula sulphurea, Erioptera uliginosa, E. needhami, Pseudolimnophila noveboracensis*, and *Dolichopeza sayi.*

The pupa has the structure characteristic of its subgenus, combining with this those details by which it is identified in the key to pupae. The spiracular yoke is illustrated in Figure 115. In the laboratory, the pupal stadium was six days. Thorax and wing sheaths were pale tawny when the pupa was two or three days old but darkened to gray about 36 hours before emergence. About 12 hours prior to emergence of the adult, the entire pupal skin darkened, as observed in other species. Throughout the pupal life, the green coloration persists in the abdominal region. The larva of *dorsalis* does not seem to construct a well-organized burrow for pupation, but the tube is evident enough to allow the cast larval skin to be recovered without much searching.

Notes on distribution.—ALBERTA—Bilby (about 30 miles west of Edmonton), 20 July; Lesser Slave Lake, 21 June. BRITISH COLUMBIA—Liard Hot Springs (milepost 496.5, Alaska Highway), 13 and 25 June and 8 July. CONNECTICUT—New Haven County, 3 and 14 July. FLORIDA—Jackson County, 6 May; Leon County, 31 March to 24 April; Liberty County, 25-26 April. GEORGIA—Hall County, 5-6 June. INDIANA—Jefferson County, 2 to 16 June and 18 to 23 August. MAINE—Hancock County, 11 June to 17 July; Piscataquis County, 14-15 July; Washington County, 25 July. MANITOBA—Aweme (20 miles southeast of Brandon), 25 June; Victoria Beach (southeast shore of Lake Winnipeg), 19 July. MARYLAND—District of Columbia (in error?), 17 May and 30 August. MICHIGAN—Alger County, 29 June; Allegan County, no date; Antrim County, 2 July; Berrien County, 11 July; Cheboygan County, 18 July; Lake County, 8 July; Livingston County, 4 June to 14 July and 11 to 30 August; Roscommon County, 1 July; Washtenaw County, 28 May to 24 June and 23 August. MINNESOTA—Clearwater County, 10-11 July; Ramsey County, 6 July. NEW HAMPSHIRE—Grafton County, 12 July. NORTH CAROLINA—Haywood County, 3 August; Macon County, 11 to 15 June; Swain County, 30 June; Transylvania County, 9 June and 8 September; Yancey County, 26 May and 1 August. NOVA SCOTIA—Halifax County, 26 June. OHIO—Hocking County, 8 June. ONTARIO—Burke Falls, 13 July. QUEBEC—Knowlton, 12-13 July. SOUTH DAKOTA—Pennington County (Black Hills), 11 July. TENNESSEE—Campbell County, 10 June.

Dolichopeza (*Oropeza*) *johnsonella* (Alexander)

Literature references.—As *Tipula annulata* Say. Wiedemann, 1828: 54.

Oropeza johnsonella Alexander. Alexander, 1930b: 279.

Dolichopeza (*Oropeza*) *johnsonella* (Alexander). Alexander, 1941a: 295; Alexander, 1942: 212, fig. 26C (hypopygium).

Original description.—"Size small (wing, male, under 10 mm.); mesonotum reddish brown, the brown praescutal stripes relatively indistinct; halteres dusky; legs pale brown, the tarsi a little paler; male hypopygium with the inner dististyle a flattened blade, the apex subtruncate, on outer margin near base with a small setiferous tubercle; gonapophyses recurved, tipped with acute spines.

"Male. Length about 8 mm.; wing 9.8 mm.

"Frontal prolongation of head and palpi dark brown. Antennae (male) relatively elongate, if bent backward extending to beyond the base of abdomen; scape honey-yellow; first flagellar segment

short, the remaining segments passing into brown. Head dark brown.

"Mesonotum reddish brown, the praescutum with three indistinct darker brown stripes. Pleura lighter brown, with vaguely indicated darker areas on anepisternum, ventral sternopleurite and ventral pleurotergite. Halteres dusky, the base of stem yellow. Legs with the coxae yellow, infuscated at base; trochanters yellow; a single (posterior) leg remains, pale brown, the tarsi a trifle paler, more yellowish brown. Wings tinged with brown, the stigma darker brown; veins brown. Venation: Cell M_1 about one-half longer than its petiole.

"Abdominal segments ringed with brown and yellow, the apices of the segments paler than the bases. Male hypopygium with the lateral portions of the tergite produced into conspicuous setiferous shoulders, the intermediate margin very gently crenulate; ventrolateral arms of tergite strongly curved, slender, not expanded outwardly, the apex acute or subacute. Outer dististyle a little longer than the inner dististyle, cylindrical, not dilated at base. Inner dististyle a flattened blade, near base on outer margin with a small tubercle set with conspicuous setae; apex of style subtruncate. Gonapophyses recurved, setiferous, the tips set with several acute spines.

". . . In its small size and general appearance, *Oropeza johnsonella* agrees most closely with *O. rogersi* Alexander, differing in the structure of the male hypopygium, especially the inner dististyle, which bears a setiferous tubercle on outer margin beyond base."

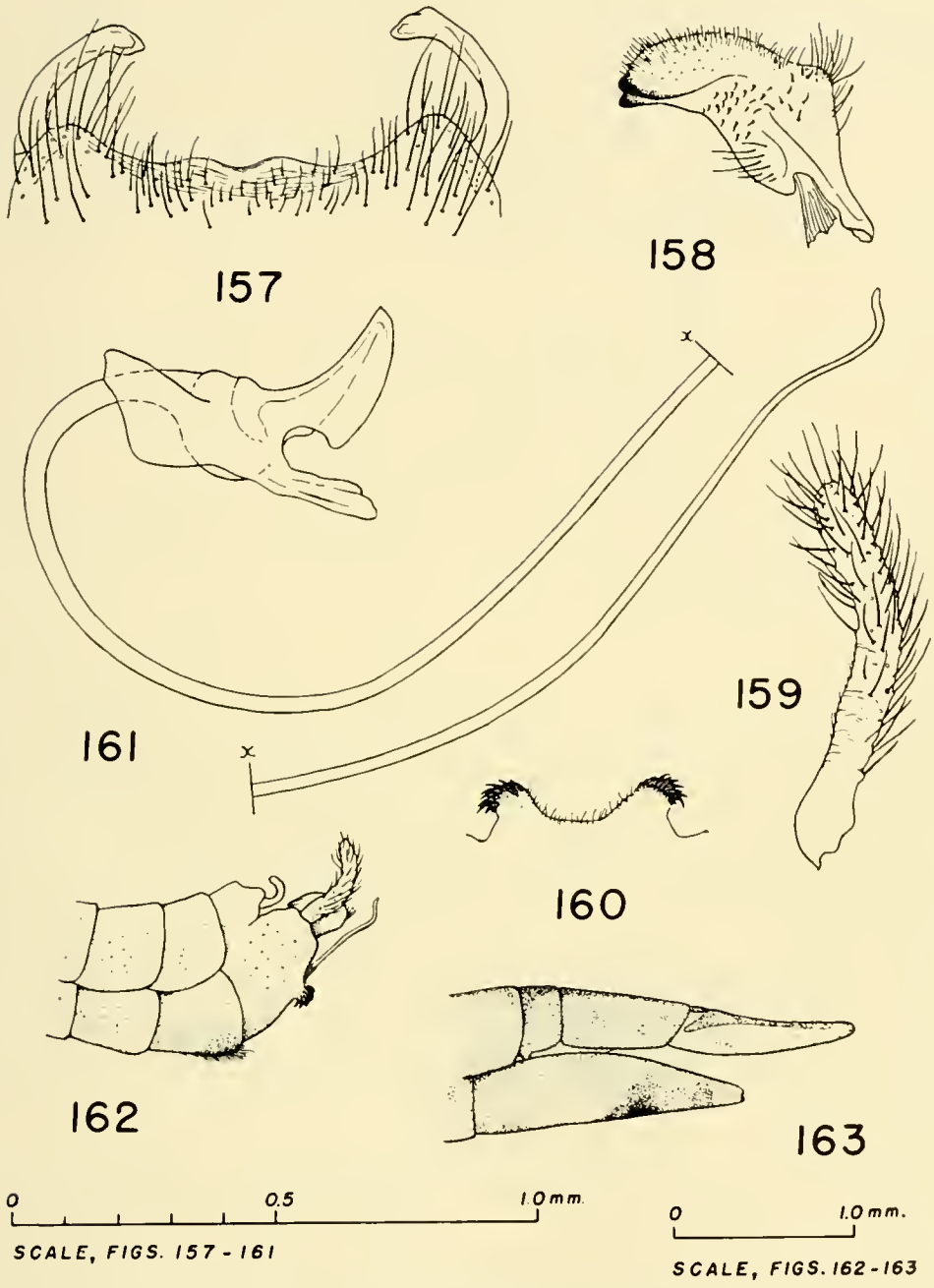
Type.—Holotype male, Riverton (northwest Burlington County), New Jersey, August 1911, C. W. Johnson. This specimen, in the Museum of Comparative Zoology, Harvard University, now consists of the pinned thorax, part of the abdomen, and head with part of one antenna. One broken wing is attached to the thorax. The hypopygium has been mounted in a drop of balsam on a celluloid square attached to the pin; but, due to curling of the celluloid, the balsam has become wrinkled and cracked, as a result of which the hypopygium is scarcely visible and thus worthless. Although the type is of no use for comparison and, in addition, is scarcely typical of the species (as will be explained later), it seems unnecessary at the present to designate a substitute type.

Diagnostic characteristics.—As one of the dusky colored species of the *obscura* group, *johnsonella* is most easily confused with

obscura, polita and *tridenticulata,* and it is difficult to identify even males without first capturing them. The golden-brown tinge and well-defined, oval stigmal spot of the wing and the presence of discernible stripes on the prescutum and spots on the thoracic pleura all aid in the recognition of this species. A good characteristic for field determination of males is the darkness of the eighth abdominal segment and contrasting paleness of the ninth, especially the sternum, coupled with the presence of a usually conspicuous tuft of black hairs at the ventro-posterior apex of the eighth sternum. This latter feature, overlooked at the time of original description of the species and found only in *johnsonella,* is shown in Figure 162.

Preserved males may be easily distinguished from all other species of the genus by the structure of the hypopygium. Of the *obscura* group, only *johnsonella* and *subalbipes* lack the toothed medio-posterior margin of the ninth tergum. Some specimens of *subalbipes* found in collections were labelled *johnsonella,* and attention was drawn to the white tarsi. Even legless specimens of *subalbipes* of the form having slender tergal arms may be told from *johnsonella* by the fact that the medio-posterior region of the ninth tergum, while it may be only two lobed, is produced caudad, in contrast to the broadly but shallowly emarginate, rather undulating margin of the ninth tergum of *johnsonella* (Fig. 157). Occasionally there is a minute median tooth, suggesting a similarity to *australis;* however, the ninth tergum of the latter has the median tooth projecting beyond the broad lobes. Differences between these two species are discussed more fully under *australis.* Female specimens, sometimes mistaken for faded *Dolichopeza venosa,* are distinguished from that species by the hypovalves: in *venosa,* there is dense sclerotization of the hypovalve from its dorsal margin to the mid-ventral line, beginning beneath about the mid-length of the tenth tergum and extending very nearly to the tip, which is abruptly paler by contrast; in *johnsonella,* the dense sclerotization is more limited to the ventro-lateral surface and is especially intense below the tenth tergum, growing less dense toward the tip of the hypovalve (Fig. 163). Also, even in faded specimens, the golden-brown tinge of the wing will usually still be present and distinguish *johnsonella.* This wing coloration rather resembles that of *similis,* females of which may be recognized by the characters stated in the key.

Descriptive comments.—The original description is fairly adequate as far as coloration is concerned. It might be well, however,



FIGS. 157-163. *Dolichopeza (Oropeza) johnsonella;* 157—ninth tergum of male, 158—left inner dististyle of male, dorsal aspect, 159—left outer dististyle, dorsal aspect, 160—gonapophyses, dorsal aspect, 161—vesica and penis, 162—terminal abdominal segments of male, left lateral aspect, 163—terminal abdominal segments of female, left lateral aspect.

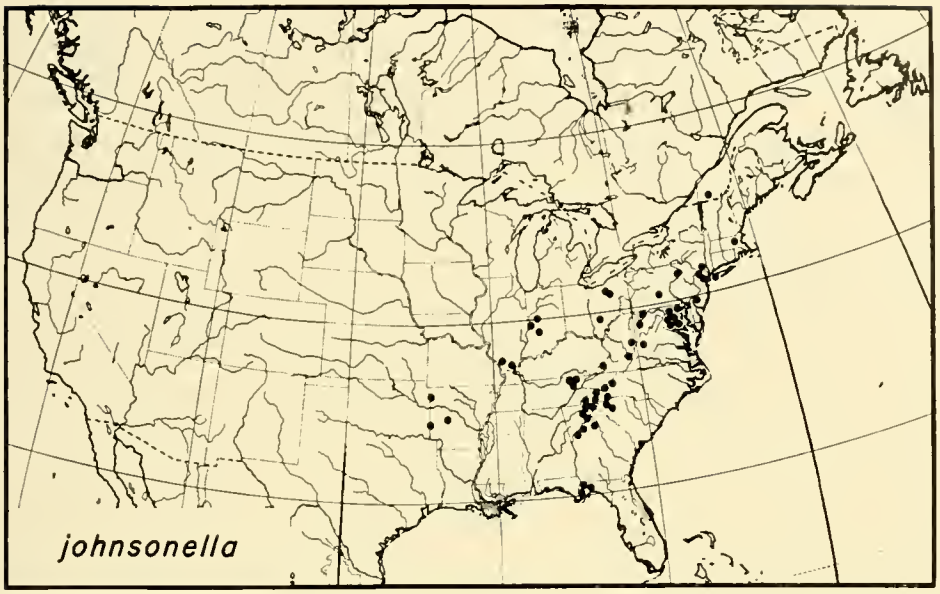
to mention that considerable variation should be expected. For example, prescutal stripes may sometimes be plainly visible, while in other specimens they may be obliterated completely; the legs may be dark brown as well as light brown; and under some conditions of preservation, body coloration of females may be so pale as to cause confusion of this species with *Dolichopeza walleyi,* until close examination of prescutum, wings and abdominal annulation is made.

Venational variations found in *johnsonella* include loss of the proximal half of the vein M_2, presence of Sc_1, presence of an extra cross-vein in cell R_3, branching of M_3 from M_{1+2} beyond the discal cell, loss of the medial cross-vein resulting in absence of a closed discal cell, and presence of a basal fragment of R_{1+2}. All these variations are uncommon, and the venation of the species in general is quite constant. The cell M_1 is not always half again as long as its petiole, as described.

Because the holotype was an autumn fly, affected by environment as described earlier in this report, the size given by Alexander is not precisely characteristic of the species. The fact is that *johnsonella* is one of the larger species of the genus, some females reaching 14 mm. in body length, with wings of equal length. Males measure from 7 to 10 mm., the wing length varying from 9 to 12 mm. In all cases the small individuals were collected in August and September. Females of the late summer generation may be as small as 9 mm. in length, with wings 10 mm. long. The difference in mean size between spring and late summer generations in this species is marked, although individuals as small as the holotype are unusual.

The characteristic structure of the male hypopygium of *johnsonella* has already been described. Variation in the ninth tergum consists of slight differences in breadth of the low, rounded lobes and of the concavity between them, minor differences in length and shape of the tip of the tergal arms, and, as already mentioned, occasional presence of a tiny median projection. The setae on the outer surface of the inner dististyle (Fig. 158) are not always concentrated upon a tubercle (compare Alexander, 1942: 213, fig. 26C) but may be more sparsely distributed over the angular bend of the dististyle.

Geographical distribution.—Previously published records indicate that the range of *Dolichopeza johnsonella* is the Appalachian region from New Jersey to South Carolina, but recent exploration



MAP 4. Range of *Dolichopeza (Oropeza) johnsonella* (Alexander). Each spot represents one or more collections within a county (United States) or at a locality.

has shown that this area is actually only a small part of the species' range. I found it common in three Indiana localities and in smaller numbers in southern Illinois and the Ozark-Ouachita Mountains region, as far west as the Arkansas-Oklahoma border. It also occurs as far north as New England and Quebec. Still, the distribution of this species is only sketchily known. It may be seen, by comparison of the distribution maps of *johnsonella* and other species of the *obscura* group, that the known range of *johnsonella* is very unlike that of any of its near relatives. However, I have seen what I consider appropriate habitats for this species in Missouri, northern Illinois, Wisconsin and Minnesota, and I believe that further collecting will establish that *johnsonella* ranges much more widely than present evidence indicates.

Habitats.—Dolichopeza johnsonella appears to be a denizen of well-shaded situations that are in most cases rocky and often drier than habitats of most species of the genus. In the single published reference to habitats of this species, Alexander (1941a: 295) lists as its haunts in western North Carolina ". . . along Neal's Creek, beneath culverts . . . in small rock caverns below the (Conestee) Falls, associated with *D. (D.) americana* Needham and *D. (O.) dorsalis* (Johnson) . . . along Hughes Ridge trail above Smokemont, 2500 ft., under darkened overhanging banks, swarming in hollows thus formed. . . ." In Indiana, I took *johnsonella* only in shaded crevices or beneath rock outcrops in limestone

and sandstone ravines; that is, never in equally dense shade in the woods nearby. My Ohio records are for similar habitats. Collections in the Ozark Mountains and Ouachita Mountains were made along rocky stream beds or on rocky hillsides. In western Florida, the habitats are not rocky but are rather like the piedmont region in many respects, both physically and biologically (Rogers, 1933: 24-25).

Localized aggregations of individuals are sometimes found, as for example along McCormick's Creek, Owen County, Indiana, where I was unable to find *johnsonella* among swarms of resting *Dolichopeza* species for great distances above and below a waterfall, yet beneath certain outcropping ledges of limestone along about a fifty-foot length of the cliff near the fall this species was almost the only one to be found and was present in great numbers. It was this aggregation, incidentally, that led to discovery of a larval habitat for the species. Less pronounced localization of *johnsonella* was noticed at other localities.

Seasonal distribution.—Except in the Florida portion of its range, *johnsonella* has two annual generations, one in June and the other in August. Most Florida specimens were taken in the early days of April. Even the northernmost records seem to represent a June generation, but there have been too few collections of this species in New England and Canada to make this clear. It is my impression, based on concentrated collecting in Indiana, that *johnsonella* reaches its peak of emergence a short while after all other species have passed their peaks. In Pope County, Illinois, in mid-July, it seemed that the local population of *johnsonella* was dwindling at the same time the second generation of *americana* and *polita* was getting underway, but I believe this situation is somewhat atypical for that latitude, especially insofar as the date is concerned. In Indiana, the spring peak of abundance of adults of *johnsonella* comes about the third week of June and the peak of the late summer generation in late August.

Immature stages.—Dissection of gravid females indicates one may lay as many as 120 eggs, which measure, on the average, .74 by .29 mm. These are measurements and counts on June specimens. Eggs laid on the nights of 21 and 22 June began to hatch on the night of 28 June.

In the near vicinity of the concentrations of *johnsonella* described above, the only bryophyte growing in any quantity was the moss *Gymnostomum calcareum*. It therefore seemed likely that this

moss was the larval habitat of the crane fly, and a large amount of the moss and its marl substrate was brought into the laboratory and placed in a terrarium. From it, there emerged during the following two weeks or so several adults of *Dolichopeza polita cornuta* and one adult of *johnsonella;* however, as I was away from the laboratory making further collections and field studies, I was unable to find the pupal skin of *johnsonella* at the time of emergence, and it had been destroyed by the time of my return. Thus, while the larval habitat is known, neither late stage larva nor pupa of *johnsonella* has yet been found. Having made a careful examination of the *Gymnostomum* moss before placing it in the terrarium and having found no larvae, I believe they must find daytime shelter in the porous marl deposited by the moss about its lower stems. It will be seen in Table 3 that *johnsonella* has been placed nearer the "dry habitat" end of the scale than would appear warranted on the basis of this one known habitat, which was quite wet. This was done because the species is so often taken as adults in situations where much drier conditions prevail. It is expected that the larva and pupa of *johnsonella* will somewhat resemble *subalbipes,* perhaps having some characteristics of *obscura.*

Notes on distribution.—ARKANSAS—Garland County, 31 July; Polk County, 30 July; Washington County, 30 July. FLORIDA—Gadsden County, 28-29 March; Leon County, 18 March and 16 to 24 April; Liberty County, 3 to 18 April. GEORGIA—De Kalb County, 19 August; Fulton County, 25 August and 24 September; Hall County, 6 June; Lumpkin County, 7 June; Oconee County, 21 August; Rabun County, 12 June; Union County, 10 and 28 June. ILLINOIS—Jackson County, 4 June; Pope County, 14-15 July. INDIANA—Montgomery County, 28 June; Owen County, 8 and 18 to 26 June; Parke County, 10 to 28 June and 30 August. MARYLAND—Baltimore County, 14 to 17 June; District of Columbia, 11 June and 9 July; Garrett County, 26 June; Montgomery County, 7 June and 18 August; Prince George's County, 29 June. MASSACHUSETTS—Middlesex County, 18 June. NEW JERSEY—Bergen County, 1 to 15 June; Burlington County, August; Essex County, June. NEW YORK—Nassau County, 27 June; Orange County, 26 August. NORTH CAROLINA—Cherokee County, 31 August; Haywood County, 29 July; Macon County, 8 to 12 June and 4 to 7 September; Swain County, 20 June; Transylvania County, 8-9 June and 8 September; Yancey County, 6 to 14 June. OHIO—Hocking County, 7 June; Portage County, 25 June; Summit County, 19 June. PENNSYLVANIA

—Huntington County, 9 July; Luzerne County, 10 July. QUEBEC —Knowlton, 20 June. SOUTH CAROLINA—Greenville County, 20 May; Pickens County, 29 June. TENNESSEE—Fentress County, 31 May to 18 June and 11 August to 3 September; Morgan County, 12 June; Scott County, 30 May. VIRGINIA—Arlington County, 11 to 25 August; Augusta County, 28 June; Fairfax County, 30 May, 5 and 16 June, and 30 August to 2 September; Giles County, 11 June to 7 July and 12 August; Wise County, 2 July. WEST VIRGINIA—Pocahontas County, 23 June; Tucker County, 24 June.

Dolichopeza (*Oropeza*) *obscura* (Johnson)

Literature references.—Oropeza obscura Johnson. Johnson, 1909: 122, pl. 15 (hypopygium; wing figured as this species is actually of *tridenticulata*); *Johnson*, 1910: 708; Alexander, 1919: 930, pl. 43 (wing); Alexander, 1920: 983-984, pl. 86 (larva figured is *tridenticulata;* pupa is *polita*); Alexander and McAtee, 1920: 393; Alexander, 1925: 172; Johnson, 1925: 33; Pierre, 1926: 11; Alexander, 1928: 57; Leonard, 1928: 698; Alexander, 1929a: 236; Alexander, 1930a: 272; Alexander, 1930c: 113; Rogers, 1930: 22-23 (includes *polita* and *tridenticulata*); Alexander, 1931a: 138; Dickinson, 1932: 212, Fig. 114 (wing) (apparently refers to *tridenticulata* and *polita pratti* only); Rogers, 1933: 49.

Dolichopeza (*Oropeza*) *obscura* (Johnson). Alexander, 1936: 280; Alexander, 1940: 620; Alexander, 1941a: 295; Alexander, 1942: 212, 214, fig. 26D (hypopygium); Rogers, 1942: 59, 121; Whittaker, 1952: 36.

Dolichopezia (*Oropeza*) *obscura* (Johnson). Rogers, 1949: 12 (typographical error).

Note: *Dolichopeza obscura* Brunetti, 1912, became a secondary homonym of *Oropeza obscura* Johnson, 1909, when the two genera were combined in 1931. Brunetti's species, from India, was also recently placed in the subgenus *Oropeza*, according to Dr. Alexander, who is renaming it.

Original description.—"Head and thorax dark brown, opaque; palpi black, antennae fuscous, the two basal joints yellow; abdomen light brown somewhat shining, the black bands at the incisures not connected on the dorsal line. Genitalia yellowish, appendages blackish; style yellow, long and very slender, curved and often extending to the base of the penultimate segment, appendages at the base of style short and armed with small black spines, margin but slightly emarginate. Ovipositor brown, cerci yellow. Halteres

yellow, knobs brown. Legs brownish yellow. Wings smoky brown, the veins and stigma a slightly darker brown, the median cubital cross-vein wanting. Length, male, 8 mm.; female, 10 mm."

Types.—Holotype male, North Adams (Berkshire County), Massachusetts, 19 June 1906, C. W. Johnson. Allotype, Hammond's Pond, near Brookline (Norfolk County), Massachusetts, 18 June 1908. Five male and one female paratypes are together with the holotype and allotype, in the Museum of Comparative Zoology at Harvard University. Of these, the males labelled Auburndale, Massachusetts, 11 July 1905, Squam Lake, New Hampshire, 14 July 1907, Norwich, Vermont, 7 July 1908, and North Adams, Massachusetts, 19 June 1906, are actually *Dolichopeza tridenticulata* Alexander. The allotype and one female paratype may also be this species, but I could not be certain at the time I examined these specimens. Another male and female, both paratypes and both *obscura*, are in the collection of Dr. Alexander, at Amherst, Massachusetts. One male bearing the same label data as the holotype, thus probably one of the original paratypes although not so labelled, is in the Snow Entomoloical Museum, Lawrence, Kansas. Two female paratypes are in the collection of the Academy of Natural Sciences of Philadelphia. Johnson based his description of *obscura* on thirty-four specimens; the present whereabouts of the twenty-one not accounted for here is unknown.

Diagnostic characteristics.—Males of *obscura* may be at once recognized by the shape of the lateral arms of the ninth tergum. In no other species are these structures widely flared apically, then emarginate at the tips (Fig. 164). The profile of the mediposterior margin of the ninth tergum is also a very useful character, having three distinct and rather widely separated teeth, the median tooth usually shorter than the others.

Even after considerable experience with this species in the field, it is difficult and not reliable to make sight identifications. *Dolichopeza obscura* too closely resembles *tridenticulata* for field recognition without capturing specimens. In most places where I have found the two species together, *obscura* has been the more darkly colored, although, particularly in the northern parts of the range, the coloration of both is nearly alike. The same might be said of their relative sizes: *obscura* in most parts of the range is slightly larger than *tridenticulata*, but in the northern states and Canada and at many localities in the highlands of the Appalachians, *tridenticulata* often reaches the size of *obscura*. The wing colora-

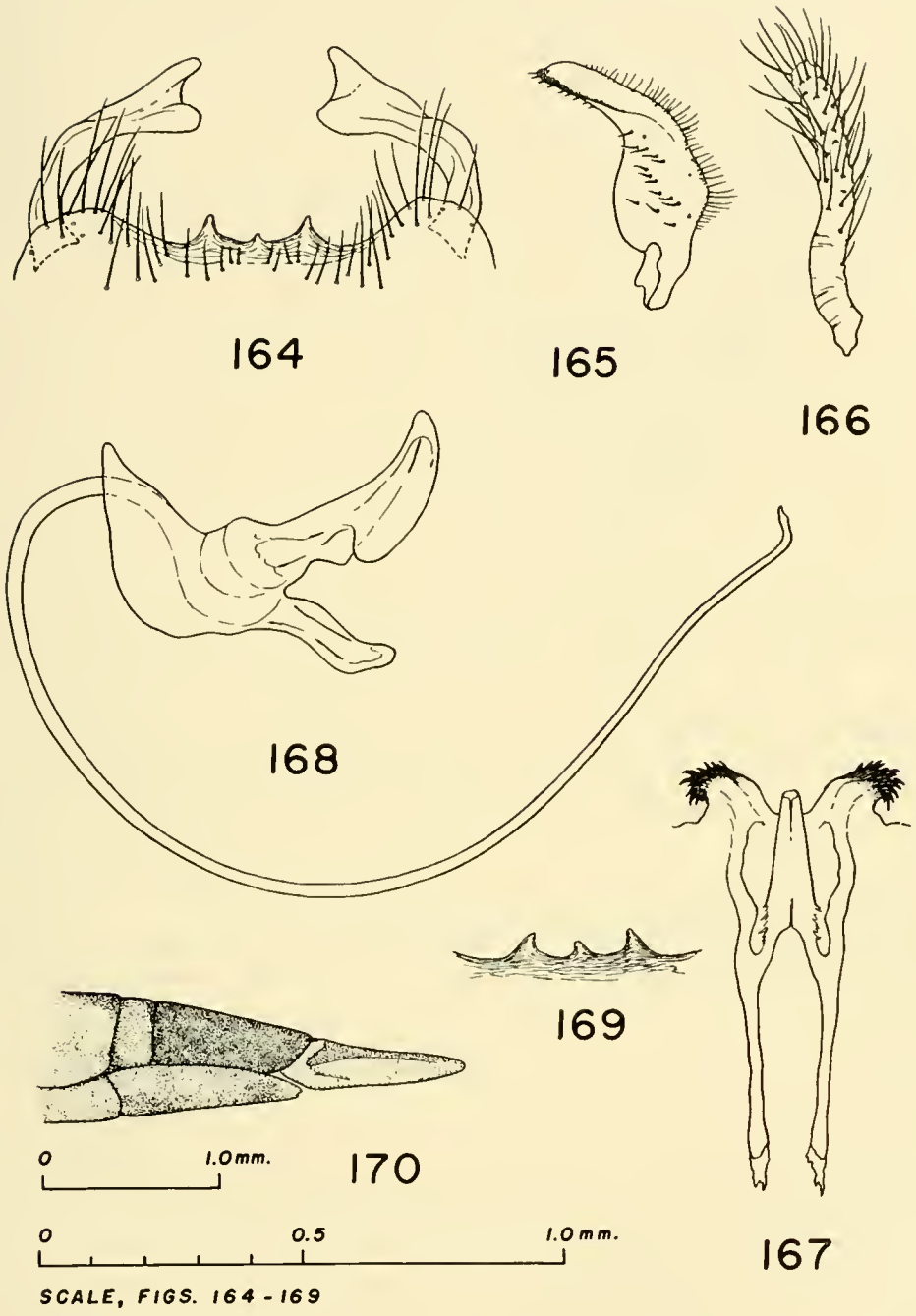
tion of *obscura* is more intense than that of *tridenticulata*, but it is almost necessary to see the two species together, knowing which is which, in order to appreciate this comparison.

Female specimens may be distinguished from *polita* by having distinct annulations on the abdomen and the prescutum dark brown and never shining. Lack of stripes on the thoracic dorsum and differences in coloration of the hypovalves of the ovipositor will separate *obscura* from *johnsonella*. Separation of *obscura* and *tridenticulata* females is very difficult. The details of coloration of the hypovalves mentioned in the key to adult females is the most reliable character I have found and is based upon study of a large number of females of known identity, as those taken in copula. A peculiarity noted in many preserved specimens is that while the cerci of *obscura* remain in alignment with the rest of the abdomen, those of *tridenticulata* are often deflected ventrad, so that the tips of the hypovalves are concealed between them. I have not discovered any anatomical reason for this difference of position of the cerci in killed flies. The color differences between *obscura* and *tridenticulata* described for males apply also to females.

Associated males are a help in identifying either *obscura* or *tridenticulata* females, as they provide at least standards for comparison of color. Habitat also, within certain limits, will aid in identification.

Descriptive comments.—Dolichopeza obscura is the darkest of the species of *Oropeza*, a very dusky-brown fly that is nearly invisible in the deeply shaded recesses beneath trees and rocks where it hides by day. The annulated pattern of abdominal coloration is distinct. The occiput of the head is a very dark grayish brown but scarcely darker than the deep brown of the pronotum and prescutum. Johnson's description of the wing coloration as "smoky brown" is apt, for the ground color does indeed suggest smoked glass. The veins and stigmal spot are dark brown, usually contrasting more with the ground color than is the case in *tridenticulata*.

Although irregularities in wing venation are not at all uncommon in *obscura*, I have not found any strong local concentrations of particular variations, such as described earlier for *tridenticulata*. Absence of the medial cross-vein is the most frequently observed abnormality of venation. Loss of sections of veins in the medial field is not unusual, and the presence of the vein Sc_1 has been noted many times. Junction of the m-cu cross-vein near the mid-length



FIGS. 164-170. *Dolichopeza (Oropeza) obscura;* 164—ninth tergum of male, 165—left inner dististyle of male, dorsal aspect, 166—left outer dististyle, dorsal aspect, 167—gonapophyses, adminiculum and adminicular rods, dorsal aspect, 168—vesica and penis, 169—medio-posterior margin of ninth tergum of male holotype, 170—terminal abdominal segments of female, left lateral aspect.

of the short M_{3+4} is quite common. One specimen was seen in which the cell M_1 was very short, its petiole correspondingly elongated, and one other had an extremely short discal cell in both wings. A short spur directed proximally from about mid-length of the m-cu cross-vein has been seen once.

Body length of males varies from 7.5 to 10 mm., the wing length from 9 to 12.5 mm. Females measure from slightly under 10 mm. to 12 mm. in body length, their wings from 10 to 13 mm. Most of the larger specimens I have seen were from the northern states and from high elevations in the central Appalachian Mountains (North Carolina and Virginia), in July and June, respectively. Smaller individuals were found in October and March collections from northern Florida and southern Georgia (Baker County).

Variation in the ninth tergum of the male consists mainly of differences in shape, length and spacing of the three acute teeth of the margin, and of fluctuations in the width, curvature and apical outline of the tergal arms. In the holotype, for example, the central tooth is deflected to one side (Fig. 169); in a specimen from Whitley County, Kentucky, there are four teeth, the usual median tooth apparently having become divided; and in a male from Westmoreland County, Pennsylvania, one of the lateral teeth has an apical bristle, while the central tooth is represented only by a bristle and the entire medio-posterior margin is atypical in form. Breadth of the basal portion of the inner dististyle varies noticeably, although the over-all shape of this structure never approaches that of any other species of *Dolichopeza*. The inner dististyle is narrower, compared to its length, in *obscura* than in the other species (Fig. 165).

In males, the antennal length is nearly equal to half the length of the body. Scape and pedicel are usually of a yellowish gray color, the flagellum darkening from that to deep fuscous at the tip.

Geographical distribution.—Collection records indicate that *obscura* is the commonest *Dolichopeza* in North America. It has been found from Nova Scotia westward to Alberta, southward to Florida and southwestward to Arkansas. I expect it will subsequently be found in swampy areas of Louisiana and Mississippi, in the Ozark Mountains of Missouri and in the rocky ravines of Iowa. The distribution map of this species shows the range fairly well outlined in eastern North America, and although I anticipated *obscura* would occur somewhat westward from Manitoba and Minnesota, I was rather surprised to find it in a forest in western Alberta, in 1957.

MAP 5. Range of *Dolichopeza (Oropeza) obscura* (Johnson). Each spot represents one or more collections within a county (United States) or at a locality.

Collections such as this and my earlier discoveries of *obscura* in Kansas and Arkansas serve to emphasize how little still is known of the geographical distribution of many of the North American crane flies.

Habitats.—The relative commonness of *obscura* in collections is very probably a reflection of its ability to flourish in a wide variety of general environments. This is the only species of *Dolichopeza* that seems equally at home in rock gorges, in moist to wet woodlands, and swamps, bogs and border vegetation of marshes. In southern Michigan, Rogers (1942: 59) found *obscura* "numerous to occasionally common in the most densely shaded birch-maple-elm and tamarack-sumac swamps. Numerous but very local in oak-hickory woods, where they were occasionally taken from the dark interior of a hollow stump or log." In his ecological study of the Tipulidae of northern Florida (Rogers, 1933), he records this species as occurring ". . . within hollow trees and dark, cool recesses of banks and cliffs." Habitats of *obscura* on the Cumberland Plateau are described as ". . . shaded, rocky, upper, talus slope brooks, 'rock-houses,' beneath overhanging banks of the upland brooks, and . . . large hollows in standing trees. Rare

in the stream-margin thickets" (Rogers, 1930: 23). In central Indiana and Ohio, I found *obscura* in sandstone ravines and rarely in limestone ravines, which seem to be drier, but more often the species was taken in upland woods. In numbers of individuals, *obscura* never equals *polita* or *tridenticulata* in the rock gorge habitats. In northern Michigan, *obscura* is extremely numerous in mesic and wet woodlands, especially in areas of deciduous forest. In the white cedar swamps and drier coniferous forests, it was always found comparatively less abundant. In the spruce forests along the crest of the Appalachians, however, *obscura* is the commonest *Dolichopeza.*

It is my impression that *Dolichopeza obscura* is the most strongly negatively phototropic member of the genus. Where this species was observed resting together with *americana* and *polita cornuta,* in Parke County, Indiana, it was in the darkest recesses of cavities shared by the three species. In other localities, also, *obscura* is found concentrated in the most intense shade available, and the flies are less readily driven from their hiding places than is the case with other species. In view of this reaction to light, it might seem surprising that *obscura* has been more often taken in light traps than any other species of its genus. On the University of Florida Conservation Reserve, at Welaka, Putnam County, Florida, Dr. R. E. Bellamy operated a light trap on most nights of the year 1946, taking six individuals of *Dolichopeza obscura* in April, three in May, seventy-five in June, five in July, two in August, none in September, and seven in October. He also obtained March, September and November records, that year, by other means. The only other *Dolichopeza* Bellamy found was *subalbipes,* which came to the light trap in much smaller numbers. It should be mentioned that Bellamy's light was very near the daytime resting places of the crane flies. It seems likely that *obscura* was present in the vicinity of his trap in great numbers and that because the species is active at night a certain number of flies randomly wandered to the light. It is, of course, possible that the reaction of *Dolichopeza obscura* (as well as other species) to light is like that of many moths, which are repelled by the bright light of the sun by day but are attracted to lights of lower intensity at night. In Cheboygan County, Michigan, I operated a light trap on a dry hill top, a few hundred yards distant from any known diurnal haunts of *obscura,* and still trapped, during July and August, half a dozen specimens. This suggests that *obscura* does not vigorously avoid light under all circumstances.

Seasonal distribution.—There is evidence, locally through much of the range, that there are two generations per year, except in Florida and in the northernmost parts of the range in the United States and Canada. In southern Michigan and in Indiana, I have found two well-marked annual generations, the first from about mid-June to early July and the second from mid-August to early September. In 1953, however, the first male of *obscura* seen at Turkey Run State Park, Parke County, Indiana, appeared on 28 May, about two weeks after the emergence of *americana* began; but there were only one or two individuals of *obscura* observed on any day until 9 June, when an abrupt increase in numbers was noted. There are Florida records for nearly every month of the year, although peaks of abundance occur in March and June. Scattered collection records indicate that *obscura* is present in greater or smaller numbers during June, July and August, in virtually any part of the known range. It is only in areas of concentrated collecting that the two-generation pattern becomes evident. The July-August trend in numbers of individuals and ratio of males to females in the northern Michigan populations suggests that there is only one, generally midsummer generation each year in that area.

Immature stages.—Eggs of *Dolichopeza obscura* from Michigan averaged .73 by .40 mm., which is unusually wide for the length. Smaller females from Florida and Georgia were found to contain shorter eggs which were comparatively more slender, measuring .65 by .28 mm. Duration of the egg stage appears to vary with temperature, for I found it to be about ten days, in northern Michigan, in late July, while Rogers (1933: 32) reports 13 to 16 days, in Florida, in March and April. Based upon dissection of teneral, gravid females, the number of eggs produced by a single fly is close to 120, perhaps occasionally more than that but probably more often fewer, I believe, for that average count includes late-stage unmatured eggs in the ovarioles, which I have reason to suspect may not be matured and laid.

A previously published account of the larva of *obscura* (Alexander, 1920: 983) described the habitat as dry moss, *Hedwigia albicans;* however, in later investigations, Rogers (1933: 49) discovered the immatures of *obscura* in "wet to moderately dry moss clumps; pupation in short tunnels between moss and wood." In my own studies, I repeatedly reared *obscura* from damp mosses, never from dry ones. I then discovered, from morphological studies of the larvae, that Alexander's notes actually applied to *tridenticu-*

lata, which species had then not yet been recognized as distinct from *obscura.* In hardwood swamps in southern Michigan, I found larvae of *obscura* numerous in the moss, *Tetraphis pellucida,* growing on decayed stumps and roots on hummocks; and less commonly they were found in mats of *Heterophyllium haldanianum* moss growing on sodden, rotten logs. Other larval habitats on the low hummocks in swampwoods were the mosses *Hypnum curvifolium* and *Leucobryum glaucum,* the latter growing much more luxuriantly there than it does more commonly on drier soil in upland woods. Although mosses growing on decayed wood are the commonest larval habitats of *obscura* wherever the species occurs, I have also reared it from bryophytes growing on soil, such as the moss, *Fissidens taxifolius,* and the liverwort, *Chiloscyphus pallescens,* both found on glacial till on well-shaded slopes.

The fourth instar larva may be identified by the presence of conspicuous transverse ridges of microscopic hairs on the dorsum of the thoracic and all abdominal segments, with the intervening rows of minute microscopic hairs long, irregular, and with their ends not clearly defined. On a typical abdominal segment, there are from front to rear four ridges about equally spaced, then a wider space, then a fifth well-marked ridge, followed by two or sometimes three fainter, more irregularly spaced ridges. The larva constructs a distinct burrow, in most mosses, in which to pupate.

Pupae of *Dolichopeza obscura* frequently occur together with those of *subalbipes* in a single mat or cushion of moss, and the pupae are very much alike. In both, the pleural spines of the second through seventh abdominal segments bear a single, long bristle, and in both the middle projections of the eighth abdominal sternum are set very close together or upon a common base. The spiracular yoke of *obscura* (Fig. 116) is, however, unlike that of *subalbipes,* as described in the key to pupae. Comparing pupae of the two species during their development, I noted that by the fourth day the pupa of *obscura* had an over-all grayish brown color, the wing sheaths somewhat paler and the thoracic dorsum brown, while the pupa of *subalbipes* was decidedly more greenish—rather a mixture of brown, gray and green difficult of description—the wing sheaths again paler but the thoracic dorsum grayish green.

Notes on distribution.—ALBERTA—39 miles south-southeast of Valley View, 10 July. ARKANSAS—Garland County, 31 July; Washington County, 30 July. CONNECTICUT—Litchfield County, 9 and 23-24 July. FLORIDA—Alachua County, 7 to 29 March, 1 to 25

April, 3 May, 10 June, 4 and 29 July, 16 October and 14 November; Escambia County, 7 April; Gadsden County, 29 March to 19 April; Hernando County, 21 March; Jackson County, 31 March, 12-13 April and 6 May; Leon County, 31 March, 14 to 24 April and 13 June; Liberty County, 27 March and 3 to 13 April; Madison County, 1 September; Marion County, 24 March to 4 April; Putnam County, 26 date records from February to November, with peak abundance in early June; Washington County, 8 June. GEORGIA—Baker County, 19 date records for January through May, July, August and October; Chattahoochee County, 11 October; DeKalb County, 4 October; Lumpkin County, 23 May; Union County, 10 and 28 June; Ware County, 1 July. ILLINOIS—LaSalle County, 7 July; Ogle County, 19 June. INDIANA—Allen County, 10 July; Jefferson County, 7 June and 1 August; Monroe County, 23 June; Montgomery County, 28 June; Parke County, 28 May to 29 June, 15 July and 1 and 30 August. KANSAS—Douglas County, 30 August. KENTUCKY — Barren County, 2 August; Whitley County, 24 June. MAINE—Cumberland County, 1 July; Hancock County, 16 August; Oxford County, 11 July; Piscataquis County, 17 July; Washington County, July. MANITOBA—West Hawk Lake, near Rennie, 4 August. MARYLAND—Baltimore County, 14 and 17 June; District of Columbia, 29 August (reported 17 May to 30 August, but these records are not supported by available specimens); Garrett County, 26 June; Montgomery County, 30 May; Prince George's County, 18 June. MASSACHUSETTS—Berkshire County, 19 June and 10-11 August; Hampden County, 3 August; Norfolk County, no date; Suffolk County, 8 August. MICHIGAN—Antrim County, 2 July; Cheboygan County, 22 June to 8 August; Chippewa County, 13 to 15 July; Emmet County, 20 July to 4 August; Gogebic County, 6 August; Huron County, 20 June; Iosco County, 22 July; Lake County, 22 June to 12 July; Livingston County, 27 May to 9 July, 31 July, and 11 August to 9 September; Mackinac County, 27 July to 7 August; Marquette County, 13 to 17 July; Oceana County, 26 July; Oscoda County, 23 to 26 June; Otsego County, 1 to 4 July; Presque Isle County, 28 July; Washtenaw County, 12 June to 3 July and 10 to 15 August. MINNESOTA—Carlton County, 5-6 August; Hennepin County, 12 June; Winona County, 7 July. NEW BRUNSWICK—Fredericton, 26 August. NEW HAMPSHIRE—Cheshire County, 16 June; Coos County, 2 to 11 July; Grafton County, no date; Merrimack County, July (?). NEW JERSEY—Bergen County, 1 to 15 June; Burlington County, 11 August. NEW YORK—Albany County, 17 June to 3 July; Cattaraugus County, 29 June to 4 July; Chenango

County, 21 July; Cortland County, 20 July; Erie County, 16 June to 10 July; Fulton County, 15 June to 20 August; Greene County, 1 July; Hamilton County, 12 and 30 July; Herkimer County, 3 July and 12 August; Oneida County, 20 June and July; Orange County, 26 to 28 August; Suffolk County, 5 July; Tompkins County, 6 July; Warren County, 26 July. NORTH CAROLINA—Avery County, 14 to 16 June; Buncombe County, 29 May and 13 June; Burke County, 14 June and 1 July; Haywood County, 30 July; Macon County, 8 to 15 and 29 June, and 24 August to 3 September; Mitchell County, 16 June; Swain County, 11 to 30 June; Transylvania County, 8 to 13 June; Yancey County, 26 May, 2 to 22 June and 1 July. NOVA SCOTIA—Guysborough County, 30 June; Victoria County, 1 July. OHIO—Hocking County, 30 May and 7 June; Portage County, 24 June. ONTARIO—Algonquin Park, 23 June to 11 July, and 21 August; Burke Falls, 14 July; Gull Lake, Muskoka District, June; Lake of the Woods, Kenora District, 4 August; Lyn (20 miles northeast of Gananoque), 10 August; Niagara Glen, 30 June; Normandale (on Lake Erie, about 10 miles south of Simcoe), 28 June; Pte. au Baril, Georgian Bay, 6 August; Severn (Lake Simcoe), 16 June; Thunder Bay (Lake Superior), 8 July. PENNSYLVANIA—Bedford County, 8 July; Centre County, 25 June; Columbia County, 15 July; Huntington County, 9 July; Luzerne County, 17 to 28 June, 5 and 10 July and 15 August; Mercer County, 25 June; Sullivan County, 27 June and 10 July; Wayne County, 18 July; Westmoreland County, no date. QUEBEC—Knowlton, 29 June to 12 July; Rigaud, 25 June. RHODE ISLAND—Washington County, 18 June and 10 August. SOUTH CAROLINA—Greenville County, 24 August. TENNESSEE—Fentress County, 11 to 19 June, 2 and 16 July and 13 August; Haywood County, 25 May; Knox County, 29 May; Morgan County, 12 June; Scott County, 30 May; Sevier County, 20 May to 12 June and 30 June. VERMONT—Chittenden County, 15 to 24 June; Essex County, 2 July; Orange County, 11 July; Rutland County, 12 July; Washington County, July. VIRGINIA—Arlington County, 11 June and 11 August; Fairfax County, 2 and 16 June and 5 September; Giles County, 18 June to 22 July, 2 and 15 to 26 August; New Kent County, 31 May; Page County, 15 July; Rockingham County, 6 July; Shenandoah National Park, 29 June and 6 July; Washington County, 2 July; Wise County, 2 July. WEST VIRGINIA—Greenbrier County, 4 July; Hardy County, 2-3 July; Pocahontas County, 23 June and 5 July; Preston County, 25 June and 5 August; Randolph County, 5 July and 6 August. WISCONSIN—Juneau County, 6 July; Trempealeau County, 7 July.

Dolichopeza (Oropeza) polita polita (Johnson)

Note: Two similar forms of *Dolichopeza*, regarded heretofore as full species, have been described as *polita* and *pratti*. Closely related to these is a third form, described below. The reasons for considering these three forms as subspecies, here, are discussed in detail in the conclusions.

Literature references.—Oropeza obscura var. *polita* Johnson. Johnson, 1909: 122-123, pl. 15 (wing); Alexander, 1919: 930; Johnson, 1925: 33; Alexander, 1929c: 297; Rogers, 1930: 22 (as part of *obscura* Johnson).

Oropeza polita Johnson. Alexander, 1931a: 138-139 (the variety redescribed as a full species).

Dolichopeza (Oropeza) polita (Johnson). Alexander, 1941a: 296; Alexander, 1942: 214, fig. 26E (hypopygium).

Original description.—"Distinguished from the typical form by having the entire dorsum highly polished. One specimen has the vein forming the anterior side of the discal cell wanting or indicated by a stub. Length, male, 9 mm.; female, 11 mm."

Redescription by Alexander (1931a):—"Generally similar to *O. obscura* Johns., differing especially in the short antennae and structure of the male hypopygium.

"Antennae much shorter than in *obscura*, if bent backward scarcely attaining the root of the haltere. Mesonotum dark brown, nitidous, without stripes. Knobs of halteres darkened. Tarsi more evidently darkened. Wings with the stigmal area paler, not contrasting strongly with the ground-color. Venation: cell 1st M_2 narrow at base. Abdominal tergites almost uniformly darkened, not conspicuously bicolorous as in several related species, the outer segment and hypopygium almost black; basal sternites a little brighter but not conspicuously dimidiate. Male hypopygium with the median region of the tergite produced into a quadrate plate that is further produced into a sharp median point; incurved lateral arms of tergite elongate, at tips dilated into spatulate dusky blades, the margins smooth. Outer dististyle black, sinuous, at base dilated and expanded, at tips nearly acute. Inner dististyle much more expanded than in *obscura*, the blade approximately as wide as long."

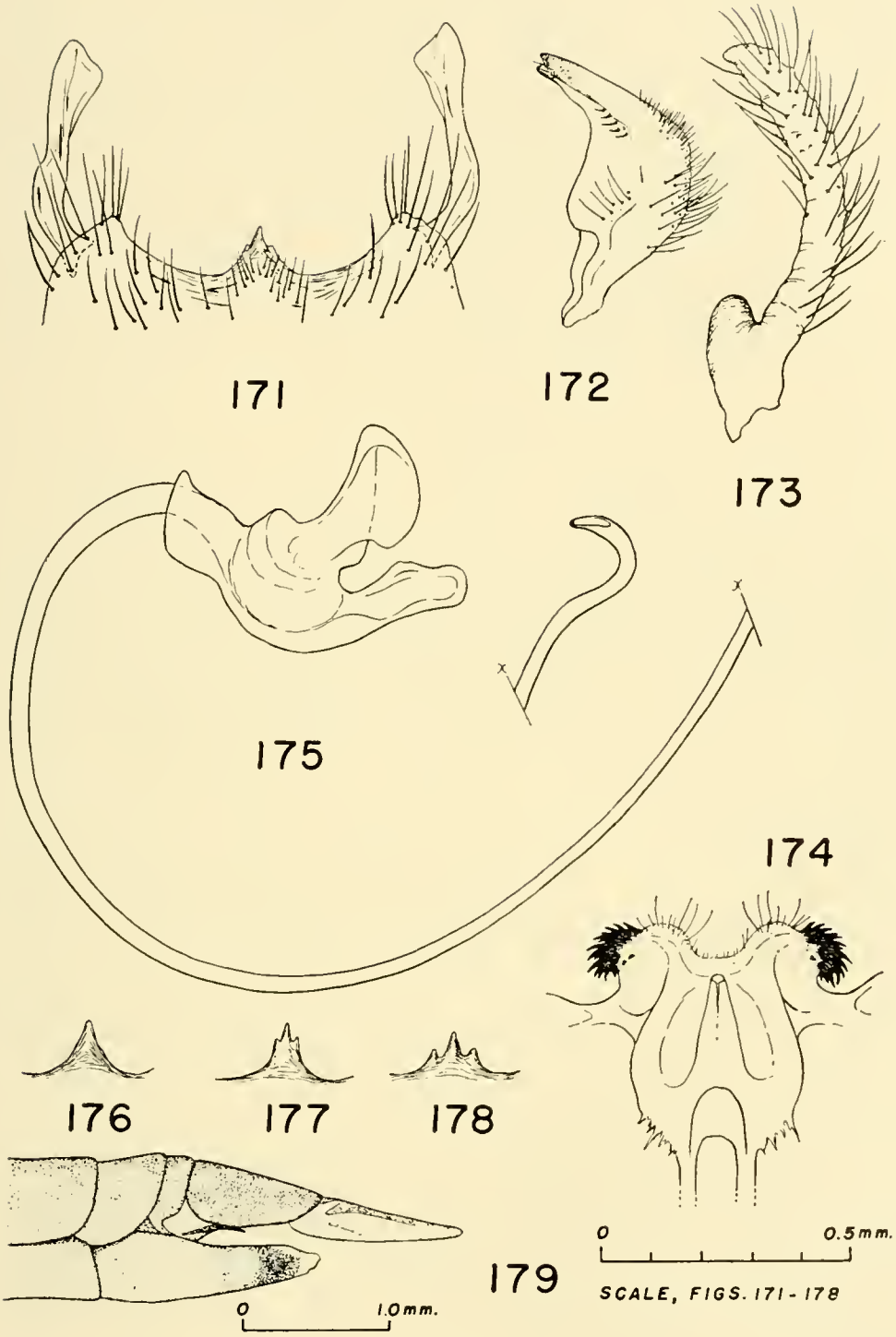
Types.—Holotype male, North Adams (Berkshire County), Massachusetts, 8 August 1907, Owen Bryant. Allotype, same data. One male and two female paratypes, together with the holotype

and allotype, in the collection of the Museum of Comparative Zoology, Harvard University.

Diagnostic characteristics.—Both sexes of this race of *polita* may be identified in the field by their dark grayish brown coloration, large size and polished appearance, the last especially evident on the thoracic dorsum, which has a somewhat paler color and higher gloss than the abdomen. Males may be recognized by the structure of the hypopygium: the tergal arms are expanded at the tips and very strongly sclerotized, nearly black, and the bulbous enlargement on the mesal surface of the base of each outer dististyle is conspicuous and usually darkened (Figs. 171 and 173). Lack of distinct abdominal annulations and the low contrast in color of the stigmal spot of the wing as compared to the ground color are characters that will aid in distinguishing *polita polita* from other species but that are found also, in greater or lesser degree, in all three forms of the species *polita.* Females of this subspecies have the subapical sclerotization of the hypovalves more intense than that of the other two races.

Descriptive comments.—The highly polished appearance of this fly, while pronounced enough to identify the subspecies, is actually a relative quality. There is a glossiness, in certain lights, in the exoskeleton of *obscura,* sometimes in *tridenticulata,* and in the other races of *polita.* Rogers (1930: 22) concluded that some degree of the polished effect is related to ". . . post-mortem changes, associated with slow and imperfect drying." I have seen a few specimens of the other forms of *polita* in which some thoracic lustre seems to have resulted from the internal separation of the flight muscles from the sclerites, but the polished appearance thus produced never equals that of the typical form of *polita,* in which it is very evident in the living flies. It is stated by Rogers (1930: 22) that "among the large series (about 100) taken of *O. obscura* are a number of specimens that now have the appearance of *O. obscura polita* with the dorsum of the thorax highly polished." Actually, this series does contain, in addition to *obscura,* several specimens of the typical race of *polita,* some of *polita cornuta,* and some apparently intergrades (see distribution map for this species).

The general coloration of this subspecies is darker than that of the other two, the abdomen especially being strongly tinged with dark green, particularly in females. In the races *pratti* and *cornuta,* the abdomen is more often of the grayish brown color found in



FIGS. 171-179. *Dolichopeza (Oropeza) polita polita;* 171—ninth tergum of male, 172—left inner dististyle of male, dorsal aspect, 173—left outer dististyle, dorsal aspect, 174—gonapophyses and adminiculum, dorsal aspect, 175—vesica and penis, 176-178—variations in medio-posterior margin of ninth tergum of male, 179—terminal abdominal segments of female, left lateral aspect.

tridenticulata, so that in males there are annulations of darker color often in evidence.

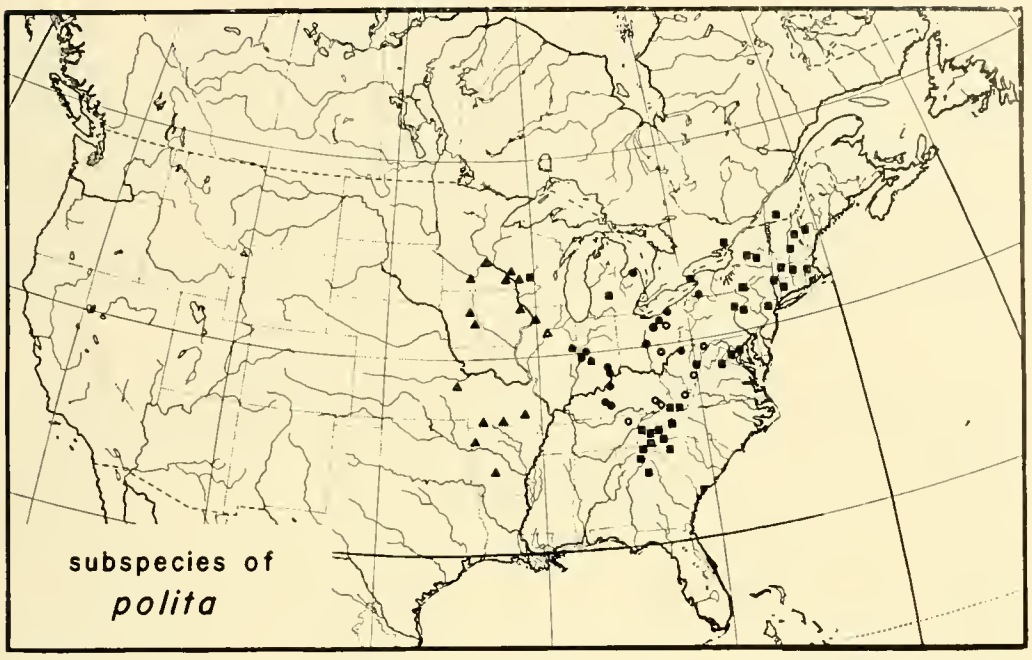
Venational variations observed in *Dolichopeza polita polita* include loss of the medial cross-vein with the discal cell remaining open and absence of this cross-vein due to closure of the distal end of the discal cell by temporary contact of the veins M_{1+2} and M_3. Absence of portions of M_2 and M_3 are not uncommon, but the abnormality figured by Johnson (1909: 122 and plate 15, as mentioned in the original description quoted above) is very unusual. Slight displacements of the m-cu cross-vein with relation to the discal cell, as well as minor fluctuations in the positions of other veins, are often seen.

Body length of males varies from 8 to 11 mm.; wing length from 10.5 to 14 mm. Females measure 8 to 12 mm.; wing length 9 to 13 mm. Throughout this species, that is, in all three races, the females are rather generally smaller than the males, although the range of body length given here does not indicate this. In all other species of North American *Dolichopeza,* the reverse is true, as it is also among Diptera in general. The size difference between spring generation individuals and those of the late summer generation is pronounced, all the larger specimens seen having been collected in June or early July.

Most variation in the male hypopygium occurs in the structure of the ninth tergum. The tergal arms vary only slightly, always within the limits of the description by Alexander, that is, with the tips widened, flattened and entire. The profile of the mediposterior margin of the ninth tergum, in contrast, varies greatly, as indicated in Figures 176 to 178. Specimens having three acute teeth in this position are not common, the form most often seen being that figured in the illustration of the typical tergum (Fig. 171). Specimens approaching either *polita pratti* or *polita cornuta* in this character are quite uncommon.

While other species of the *obscura* group have comparatively long antennae, in the males, the antennae of this and the other races of *polita* are short for the over-all body size, as emphasized by Alexander.

Geographical distribution.—Although ranging southward to Georgia along the eastern slopes of the Appalachian Mountains, this race is, I believe, the most northern of the three in the character of its distribution. The central Michigan and west-central Wisconsin localities (see distribution map) seem out of place and are in-



MAP 6. Range of *Dolichopeza (Oropeza) polita* sspp. Squares—*polita polita* (Johnson); solid circles—*polita cornuta* new subspecies; hollow circles—areas of intergradation between *p. polita* and *p. cornuta;* solid triangles—*polita pratti* Alexander; hollow triangle—area of intergradation between *p. cornuta* and *p. pratti.* Each spot represents one or more collections within a county (United States) or at a locality.

deed difficult to explain. As *polita polita* seems less bound to rocky ravine habitats in the northernmost parts of its eastern range than is either of the other two races, I believe it may extend westward from New England, across southeastern Canada, where such habitats are rare, to connect with the Michigan and Wisconsin populations. Further collecting in the northern Great Lakes area is necessary to show the true relationships of the races in the northern parts of their ranges. Where this form occurs together with *polita cornuta* (hollow circles on the map), intergrades are usually found, as already indicated for the eastern Tennessee locality. In Hocking County, Ohio (the southern of two hollow symbols shown in that state), only two specimens from a sample of 101 were of the *polita polita* type, while in the northern part of Ohio (Portage County) the two forms may occur in almost equal numbers, without intergrades. This problem is discussed in detail in the conclusions.

Habitats.—Through the greatest part of its range, *polita polita* is found in rock gorges, in the shade of undercut sandstone or limestone cliffs, and in darkened crevices between or beneath boulders in the mountainous areas. In the northeastern part of the United States, however, it occurs in much smaller crannies, such as among

boulders of rather small size on wooded slopes and along mountain brooks. While this race seems to have somewhat higher moisture requirements than either of the other races of *polita*, I have taken it occasionally in shaded niches having no evident moisture and located a hundred yards or more from any source of water. Alexander (1929c: 297) described habitats of this fly in Taconic Park, Columbia County, New York, very similar to those in which I have collected it.

Seasonal distribution.—In only a few localities is there any evidence of two annual generations. In Eaton County, Michigan, I found the first emergence of adults to take place around the middle of June and the second from mid-August to early September. In the eastern states, the collection records are scattered, so that there is no evident pattern of seasonal distribution. There are records for late May to the end of August, with the greatest number of specimens having been taken in July. The earliest dates are for southern Ohio and the southern Appalachian Mountains (30 May and 5 June, respectively), but there are records for only a few days later as far north as Quebec.

Immature stages.—Eggs of *Dolichopeza polita polita* laid by females of the late summer generation, in Eaton County, Michigan, averaged .75 by .30 mm. in size, with very short, slightly curled terminal filaments. A single teneral female contains about 110 eggs that are matured or nearly so. Of eggs laid on 17 August, the first began to hatch on 24 August, and many were hatched by the next day. The first molt came about 17 days later.

Larval habitats of this subspecies include the mosses *Campylium chrysophyllum, Desmatodon obtusifolius, Gymnostomum calcareum* and *Myurella careyana* and the hepatic *Scapania nemorosa.* All these bryophytes were growing on slightly moist to damp, shaded sandstone, except the *Gymnostomum*, which was wet. Pupal skins of *polita polita* and/or *polita cornuta* were found in the mosses *Eurhynchium serrulatum* and *Hypnum* sp. growing on damp, trapped soil on a sandstone cliff in Portage County, Ohio; and in Eaton County, Michigan, larvae were found in the moss *Plagiothecium roeseanum* growing under similar conditions.

Larvae of *polita polita* closely resemble those of *tridenticulata* but are larger, often attaining 18 mm. in length. I am so far unable to distinguish the larvae of the three races of *polita*, but separation of any of these from *tridenticulata* may be accomplished by com-

parison of the pleural regions of the eighth abdominal segments, as stated in the key to larvae.

The pupa may be recognized by having the tracheal connection between the thoracic breathing horn and the mesothoracic spiracle convoluted, as well as by the characteristic form of the spiracular yoke (Figs. 107 and 117). Before the final darkening just prior to emergence of the adult, the pupa has a dark grayish green color, the thorax and wing sheaths light brown.

Notes on distribution.—CONNECTICUT—Litchfield County, 24 July and 19 August. GEORGIA—DeKalb County, 19 August; Lumpkin County, 5 June; Union County, 28 June. KENTUCKY—Letcher County, 3 July (includes intergrades with ssp. *cornuta*). MAINE—Oxford County, 11 July. MARYLAND—District of Columbia, 25 August; Garrett County, 26 June (also intergrades with ssp. *cornuta*). MASSACHUSETTS—Berkshire County, 8 and 11 August; Norfolk County, June; Worcester County, no date. MICHIGAN—Eaton County, 3 to 14 June and 16 to 30 August. NEW HAMPSHIRE—Coos County, 2 and 20 July; Grafton County, 5 July. NEW JERSEY—Essex County, June. NEW YORK—Broome County, 13 July; Columbia County, mid-August; Hamilton County, 12 July; Herkimer County, 3 July. NORTH CAROLINA—Burke County, 14 and 21 June and 1 July; Haywood County, 25 to 30 July; Macon County, 11 to 13 June and 23 August; Swain County, 30 June; Transylvania County, 14 June. OHIO—Hocking County, 30 May, 6-7 June and 31 August (also intergrades with ssp. *cornuta*); Portage County, 24-25 June and 14 July (ssp. *cornuta* also here). ONTARIO—Gananoque, 8 July. PENNSYLVANIA—Luzerne County, 27 June and 5 to 10 July; Wyoming County, 15 July. QUEBEC—Knowlton, 12 June, 12 and 29 July. SOUTH CAROLINA—Greenville County, 7 June. TENNESSEE—Fentress County, 22 July to 14 August (includes intergrades with ssp. *cornuta*); Sevier County, 30 June. VIRGINIA—Arlington County, 25 August; Giles County, 21 June to 13 July and 1 August (includes intergrades with ssp. *cornuta*); Grayson County, 29 June and 7 August; Shenandoah National Park, 6 July; Washington County, 2 July; Wise County, 2 July (includes intergrades with ssp. *cornuta*). WEST VIRGINIA—Pocahontas County, 5 July (includes intergrades with ssp. *cornuta*); Randolph County, 5 July. WISCONSIN—Juneau County, 6 July.

Dolichopeza (*Oropeza*) *polita pratti* Alexander
(new combination)

Literature references.—*Dolichopeza* (*Oropeza*) *pratti* Alexander. Alexander, 1941b: 192-193.

As *Oropeza obscura* Johnson. Dickinson, 1932: 212 (part).

Original description.—"Belongs to the *obscura* group; general coloration of mesonotum opaque brown, without clearly defined stripes; legs dark; wings with a brownish tinge, the oval stigma a little darker brown; vein Sc_1 preserved; abdominal segments bicolored; male hypopygium with median area of tergite narrowly produced into a tridentate lobe; lateral tergal arms appearing as narrow spatulate blades; outer dististyle a little dilated on basal portion, the apex a short, spinous point; inner dististyle deep, its rostral prolongation long; aedeagus simple, unarmed.

"Male. Length about 8-9 mm.; wing 10-10.5 mm.; antenna about 2.8 mm.

"Frontal prolongation of head brownish black; palpi dark brown. Antennae with scape brownish yellow; pedicel light yellow; flagellum black; verticils of flagellar segments coarse. Head dark gray.

"Mesonontum brown, the surface of praescutum opaque, the posterior sclerites more nitidous; in some cases the praescutum with faint indications of lighter stripes. Pleura paler brown. Halteres dusky.

"Legs with the coxae pale brown; trochanters obscure yellow; remainder of legs brown, including the tarsi.

"Wings with a brownish tinge, the oval stigma a little darker brown; prearcular field a very little brightened; veins brown. Venation: Sc_1 preserved, Sc_2 ending opposite or just beyond the origin of Rs; petiole of cell M_1 exceeding m.

"Abdominal tergites obscure brownish yellow to testaceous yellow, the lateral margins and incisures darkened, on the outer segments and hypopygium the dark color including all of the segments; basal sternites yellow, the incisures narrowly darkened, the outer segments more generally suffused. Male hypopygium with the median area of tergite produced into a narrow lobe, the apex of which is further toothed, usually tridentate, with the central point longest; lateral tergal arms with outer blades expanded into weak spatulae, in some cases these only a little wider than the arms. Outer dististyle a little dilated on basal portion, the apex a short spinous point. Inner dististyle with the blade deep, the rostrum

long-produced, its apex weakly bidentate. Aedeagus simple, unarmed."

Types.—Holotype male, St. Paul (Ramsey County), Minnesota, 14 September 1940, H. D. Pratt. Five male paratypes with same data. All are in the collection of Dr. C. P. Alexander at Amherst, Massachusetts.

Diagnostic characteristics.—This subspecies may be recognized as belonging to the *polita* complex by the structure of the male hypopygium and, in the female, by the coloration, specifically the weak or absent abdominal annulations and the low contrast between stigmal spot and ground color of the wing. From the typical race, it differs in lacking the polished appearance in both sexes; furthermore the tergal arms are less densely sclerotized and the basal portion of the outer dististyles less expanded and darkened than in *polita polita.* The configuration of the tergal arms will distinguish *polita pratti* from *polita cornuta,* for while these structures are widely flared at about mid-length and narrowed at the tip in *polita cornuta* they are nearly always widest at the tip in *polita pratti.* The acute apex and expanded base of the outer dististyles will at once separate this fly from *tridenticulata,* the only species with which it might be confused on the basis of other characters of the male hypopygium; *polita pratti* is also noticeably the larger of these two in the areas where they are found together.

Descriptive comments.—Although the abdominal segments are darker at the edges, as described (and this applies to males, very rarely to females), the annulation as in the other races of *polita* is indistinct, never as in other species of the *obscura* group. The brownish color of the thoracic dorsum seems to contain a trace of red or yellow, the prescutum more nearly resembling that of *tridenticulata* than of *obscura,* which is brown. The tinge of the wings of *polita pratti* is grayish brown, fainter than the smoky brown of the wing of *obscura.*

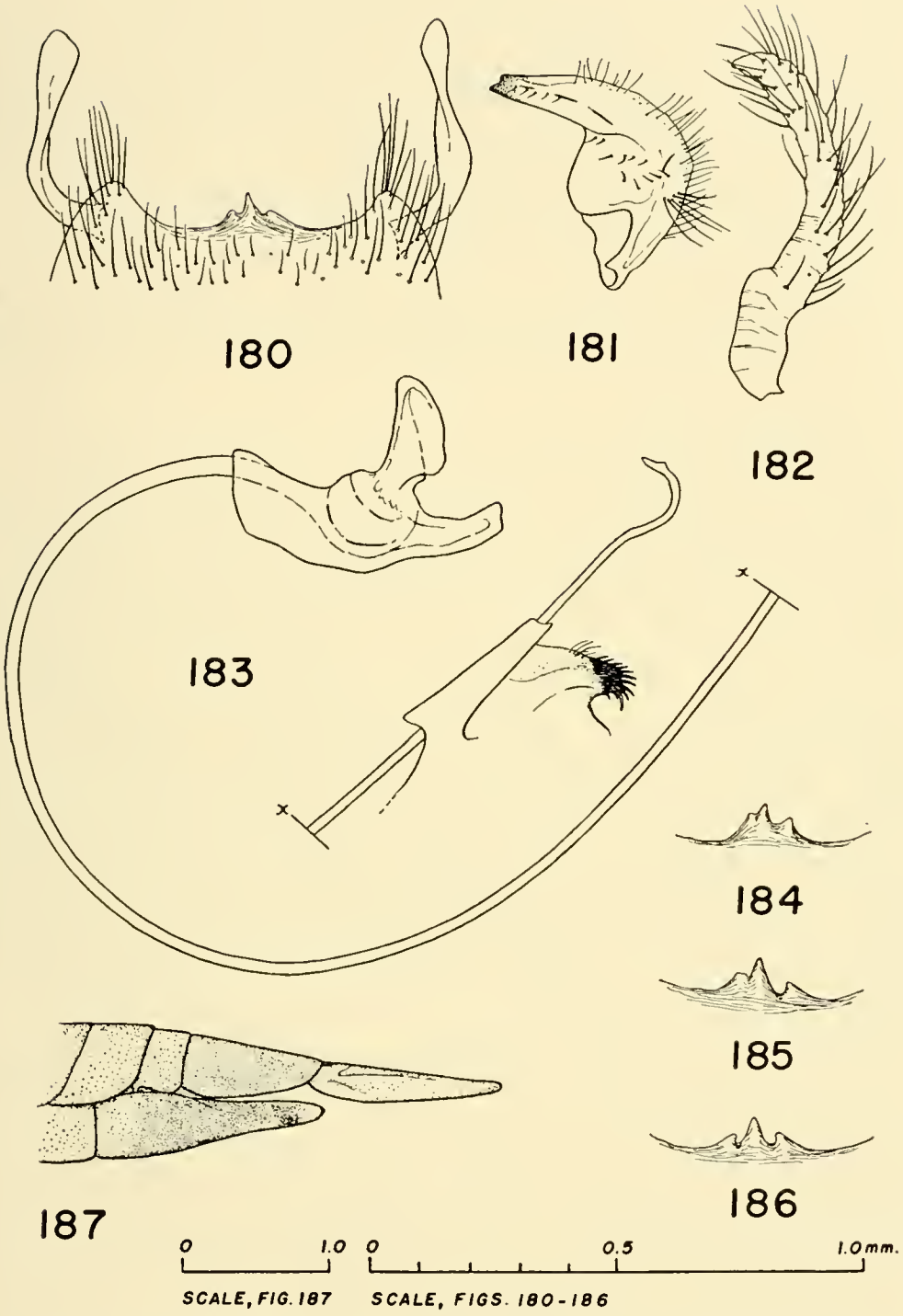
Preservation of the vein Sc_1 mentioned in the original description is an individual variation. Most specimens seen lack this vein and have wing venation characteristic of their subgenus. Other venational variations observed include loss of the medial cross-vein, the vein R_3 incomplete apically, minor displacements and interruptions of the branches of the media, and a very short cell M_1 with correspondingly lengthened petiole, M_{1+2}.

Body length of males is about 8 to 11 mm., and the wing length varies from 10 to somewhat over 13 mm. in the specimens seen.

Females are slightly smaller than males, on the average (this is the case in more than a dozen mating pairs examined), measuring 9 to 11 mm. in body length and 9.5 to 12 mm. in length of wing. The smallest measurements recorded were those of the types, which, it will be noted, were taken in September. Late August individuals collected in Kansas were smaller than the June and July specimens but larger than the types.

Variation in the shape of the medio-posterior margin of the ninth tergum of the male is extreme, exceeding even that found in the typical race. In this characteristic, *polita pratti* is much like *polita polita,* although except for the fact that the tergal arms are widest at the tip this subspecies otherwise more nearly resembles *polita cornuta* in hypopygial characters. Among the six types (all males) there are no less than four distinct shapes of the toothed medio-posterior margin of the ninth tergum. In Trempealeau County, Wisconsin, I collected a group including forty males, among which there were twelve major shapes of this structure, some extremes of which are shown in Figures 184-186. Within this same group of flies were found six kinds of tergal arms and three main classes of outer dististyles, the last on the basis of the degree of protrusion of the bulbous basal enlargement, which sometimes approaches the condition found in *polita polita* (compare with Fig. 182). Assigning letters to each different shape of these three structures, I set down a formula describing each of the forty flies. There were only six duplications in the resulting three-letter formulas; that is, there were thirty-four combinations on the basis of variation in these three characters only!

Geographical distribution.—Dolichopeza polita pratti is known from western Wisconsin, southern Minnesota, Iowa, northwestern Illinois, the Ozark-Ouachita Mountains region of Missouri and Arkansas, and eastern Kansas. Specimens regarded as intergrades with *polita cornuta* were found in a large collection including both races from Starved Rock State Park, La Salle County, Illinois. It is interesting that the transition from *polita polita* in Juneau County, Wisconsin, to *polita pratti* in nearby Monroe County should be so abrupt. The two localities represented by these collections are only 36 miles apart, and I sampled both habitats on the same day. It seems likely that northeastern Minnesota is within the range of the species *polita,* but of which subspecies I am not certain. I am confident that *polita pratti* will be found in eastern Oklahoma, and it may reach western Iowa and parts of Nebraska and South



FIGS. 180-187. *Dolichopeza (Oropeza) polita pratti;* 180—ninth tergum of male, 181—left inner dististyle of male, dorsal aspect, 182—left outer dististyle, dorsal aspect, 183—vesica, penis, gonapophysis and adminiculum, left lateral aspect, 184-186—variations in medio-posterior margin of ninth tergum of male, 187—terminal abdominal segments of female, left lateral aspect.

Dakota along the Missouri River. Surely also it occurs much more widely in the states from which it is already recorded.

Habitats.—All the known habitats are characterized by outcropping rock or large blocks of broken rock, in nearly all instances along streams, although the particular crannies in which the flies were taken were often well removed from the water. In fact, these cavities were in some cases apparently dry, but they were invariably deeply shaded so that any available moisture in the air would be conserved. Some of the flies were found beneath culverts, in cavities under earthen banks and in various other types of niches, where these occurred within the general rocky ravine or rocky hillside habitat.

Seasonal distribution.—Little is known about the seasonal occurrence of *Dolichopeza* in the western parts of the range of the genus, for too few collections have been made. In two successive years I obtained fair numbers of *polita pratti* in the upper Mississippi valley region in early July, and it was found numerous in central Iowa during the latter part of June by Dr. Jean Laffoon. Therefore, the capture of the type series in the same general area in September strongly suggests the usual two generations per year cycle. Dr. Rogers obtained a few specimens of this form in Taney County, Missouri, in mid-June, and I found them in the Ozark-Ouachita region in small numbers at the end of July and in Kansas late in August. The collection of both sexes in fair numbers in Kansas on 30 August indicated a period of emergence well underway. Accordingly, there would appear to be two annual generations of *polita pratti* in the southern part of its range, as well.

Immature stages.—Eggs taken from preserved females show the very short terminal filament characteristic of the species *polita*, the filament only slightly curved in this race. Larvae of this form have not been seen but probably closely resemble those of the other subspecies. Pupal skins were found projecting from a thin mat of the moss *Tetraphis pellucida* and a powdery lichen on the underside of a sandstone outcrop. Protected from rainfall and from seepage, this larval-pupal habitat was rather dry at the time of collection of the pupal skins. Of 17 skins recovered, four females had the middle spinous processes of the eighth abdominal sternum slightly separated at the base, that is, not divergent from a common base, and one male lacked one of these projections. Only one specimen had any spinous processes on the fourth abdominal sternum, and this was on one side

only. Among 11 female skins and 6 of males, there was uniformity of shape of the spiracular yoke, as Figure 117.

Notes on distribution.—ARKANSAS—Garland County, 31 July; Washington County, 30 July. ILLINOIS—Carroll County, 7 July; La Salle County, 7 July. IOWA—Boone County, 21 to 25 June; Jackson County, 8 July; Webster County, 30 June. KANSAS—Douglas County, 30 August. MINNESOTA—Blue Earth County, 8 July; Ramsey County, 14 September; Winona County, 7 July. MISSOURI—Barry County, 29 July; Carter County, 6 June; Taney County, 10 to 20 June. WISCONSIN—Monroe County, 6 July; Trempealeau County, 7 July.

Dolichopeza (*Oropeza*) *polita cornuta*, new subspecies

Literature references.—As *Dolichopeza* (*Oropeza*) *polita* (Johnson). Foote, 1956: 221.

The name *cornuta* is selected to describe the lateral arms of the ninth tergum, which, being widened near the base and narrowed at the tip, suggest horns.

Description.—*Dolichopeza* (*Oropeza*) *polita cornuta* is olive-brown in general coloration and, depending upon preservation, may appear light to rather dark olive-brown, although not as dark as *polita polita*. Thoracic dorsum, especially the prescutum, more reddish brown, opaque and usually dull. Abdomen faintly annulated with fuscous. Occiput of head, the maxillary palps, and flagellar portion of the antennae gray-brown to dark gray. Scape yellowish brown and pedicel straw yellow. Legs brown. Wings tinged with pale grayish brown, the stigmal spot only slightly darker than the ground color. Lateral arms of ninth tergum of male flattened and expanded at about their mid-length but narrowed apically to blunt, horn-like tips. From the median lobe of the ninth tergum, three slender, acute teeth, the center tooth slightly the longest, project caudad, nearly parallel. Bases of the outer dististyles are expanded, forming a bulbous enlargement on the mesal surface of each, the enlargement abruptly paler than the rest of the dististyle. Tenth tergum and most of hypovalve of female ovipositor about equally heavily sclerotized, the cerci and tips of the hypovalves paler by comparison. Body length of holotype male 10.5 mm.; wing 12.5 mm. Allotype length 12 mm.; wing 13.5 mm. Flies of the late summer emergence may be smaller, as indicated below.

Types.—Holotype male, Turkey Run State Park, Parke County (Field Catalogue Number 6), Indiana, 20 June 1950, G. W. Byers.

Allotype, same data as holotype. Paratypes, forty males and ten females from the type locality, collected during the spring period of emergence. The holotype, allotype and most of the paratypes are in the University of Michigan Museum of Zoology, Ann Arbor, Michigan. Two paratypes have been sent to the United States National Museum, Washington, D. C. Because I have hundreds of specimens from several localities and in varying states of preservation, it seems reasonable to limit the paratypic series in some way; hence the selection of fifty topotypes in good condition and from the same seasonal generation as the holotype.

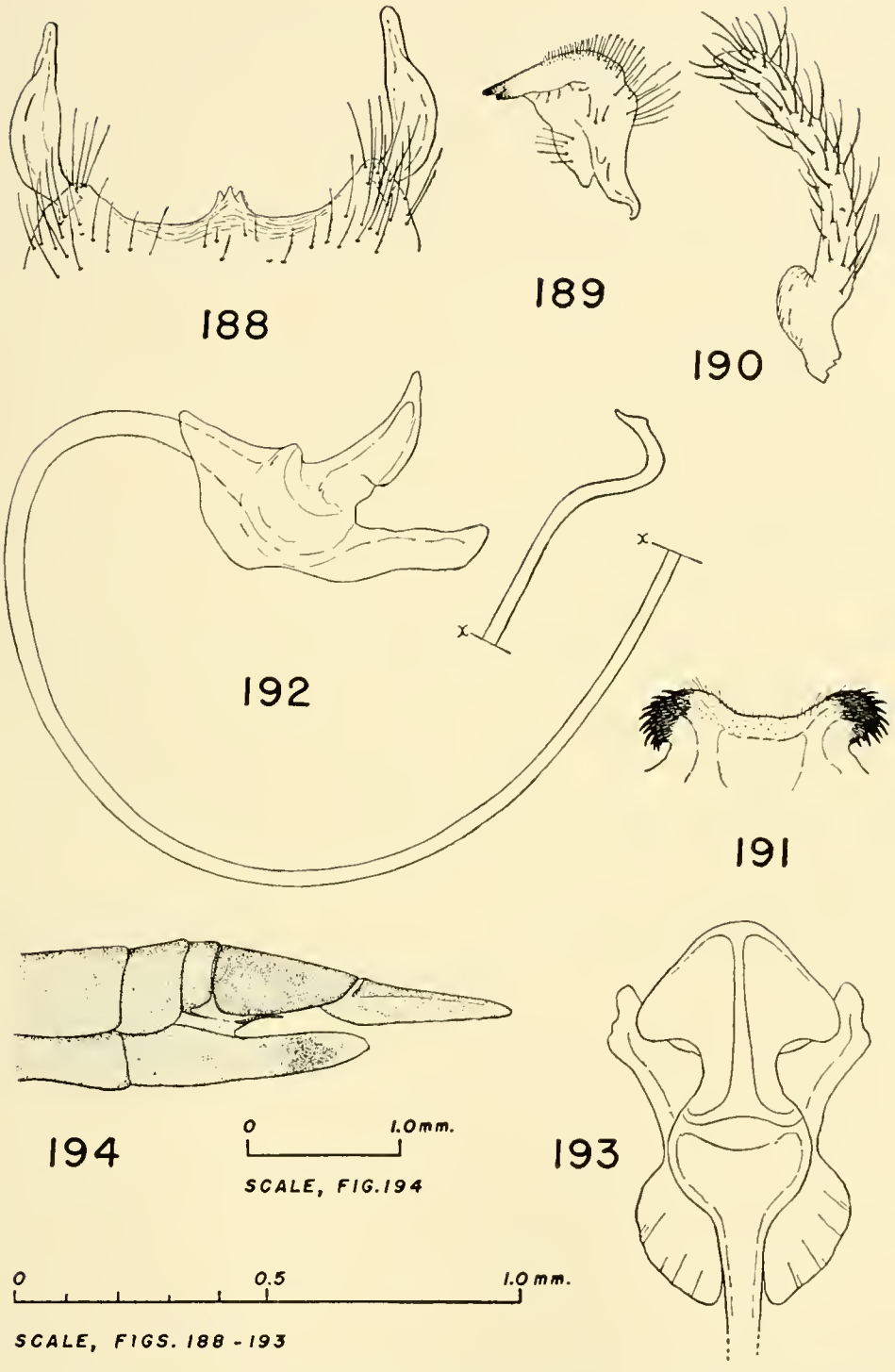
Descriptive comments.—Venational abnormalities are common in this race, although most of these are limited to the medial field. Loss of the medial cross-vein is not unusual, and I have seen many different patterns of fragmentation of the branches of the media. Rarely, wings having a well-developed Sc_1 or R_{1+2} have been found. In one male, the m-cu cross-vein has shifted so as to intersect the media at its first division.

As in the other subspecies of *polita*, females of *polita cornuta* are usually slightly smaller than males of the same generation in the same vicinity. Including both spring and late summer generations, measurements of males range from 9 to 11 mm., wing 11.2 to 13.8 mm.; females, from 9 to 12 mm., wing 9.5 to 13.5 mm.

In male hypopygial characteristics, *polita cornuta* is the most uniform of the three races. There is some variation in the length of the teeth on the ninth tergum, and the central tooth may be more or less depressed below the plane of the other two. The expanded portion of the outer dististyle is somewhat less developed than in the typical race but usually exceeds that of *polita pratti.* It is never darkly colored, as in *polita polita.* Often the mesal surface of the outer dististyle just beyond the bulbous basal enlargement lacks hairs, a condition that has also been seen in the other subspecies. The shape of the tergal arms, which most readily identifies this subspecies, is extremely constant, although the width of the flared portion may vary slightly.

The antennae are short, as in the other two races.

Geographical distribution.—Dolichopeza polita cornuta ranges from the upper "thumb" region of the Lower Peninsula of Michigan and from western New York state southwestward to eastern Illinois, southern Kentucky, and the Appalachian foothills of eastern Tennessee and western slopes of the Appalachians in Virginia and West Virginia. This area is rather well surrounded by the



FIGS. 188-194. *Dolichopeza (Oropeza) polita cornuta* new subspecies; 188—ninth tergum of male, 189—left inner dististyle of male, dorsal aspect, 190—left outer dististyle, dorsal aspect, 191—gonapophyses, dorsal aspect, 192—vesica and penis, 193—vesica and its apodemes, dorsal aspect, 194—terminal abdominal segments of female, left lateral aspect.

ranges of *polita polita* and *polita pratti* and by absence of apparently suitable habitats to the soutwest. I therefore believe that the range as indicated on the map is very close to the actual range in nature. The relationship of *polita cornuta* to the eastern subspecies is confusing at several localities, and it will be interesting to see how the ranges of the two will meet or overlap in such places as western Pennsylvania, where further collecting must be done. I have seen a specimen from Luzerne County, Pennsylvania, that is in many ways like *polita cornuta,* but because there are also certain dissimilarities and because the specimen is only one from a very large sample I have regarded it as an atypical individual and have not indicated it on the map.

Habitats.—Localities from which *polita cornuta* is known are characterized by rock outcrops or rock-walled ravines, providing deep shade for the adults and retaining moisture sufficient to grow mats or clumps of mosses for the immature stages. Adults are sometimes found in great numbers in darkened recesses beneath projecting ledges of rock. Where the space between outcropping rock and the ground below is great—say, more than ten feet, this and other species of *Dolichopeza* occurring with it are not likely to be found. But when the sheltering rock is close above the ground, providing deeper shade and protecting the flies from desiccation, they are likely to congregate. In places where I have most often collected this fly, it only rarely ventures up out of the cool ravines, although it sometimes may be found in parts of the ravines where no mosses could be seen.

Seasonal distribution.—There is abundant evidence of a two-generation annual cycle. In Indiana, where most intensive studies of this subspecies were carried on, the start of the spring period of emergence of adults closely follows that of *americana,* the peak being reached about the end of May. In 1953, for example, a particular cranny was visited every day so that comparative abundance of the various species could be estimated, although occurrence was noted throughout the area. First individuals of *polita cornuta* appeared on 23 May, when ten flies were counted. This was about a week after the onset of emergence of *americana.* Thereafter. population build-up was rapid, and by 28 May I estimated numbers in excess of 150 flies of this form. On 30 May, peak numbers were present—probably well over 200 individuals of *polita cornuta* in the one small cranny mentioned. A single sweep of the collecting net yielded 61 males and 52 females, as well as 29 flies of other

species of *Dolichopeza,* on 1 June; by 9 June only 15 *polita cornuta* could be found at this site, and a few individuals of the spring generation were still present on 11 July. The late summer peak, in Indiana, falls in the first two weeks of August, *polita cornuta* again appearing shortly after *americana* and before any other species of *Oropeza.* On 3 August, great numbers of these flies were collected in Jefferson and Jennings counties, in southern Indiana; earlier collecting in that vicinity clearly showed these to belong to a second annual generation.

Immature stages.—Eggs of *polita cornuta* are about the same size as those of *polita polita*, being .75 by .30 mm., on the average, depending on the size of the female fly. There is a very short terminal filament, which projects slightly and then undergoes about one complete, circular coil; the filament is thus a little longer and more coiled than that in either of the other subspecies. Eggs from females of the spring generation were placed in a rearing dish on 24 June, and second generation adults appeared on 17 August.

The larvae are ordinarily green in color by reason of the lack of any dense coating of microscopic hairs to obscure the pigment in the body contents. Most of the minute hairs on the body are extremely short and occur singly, a characteristic found elsewhere only in *tridenticulata* and the other races of *polita.* On the eighth abdominal segment of the larva, the dorsal microscopic hairs are abruptly longer than any others on the body, which gives a somewhat darker appearance to the hind part of the larva and a sharp contrast to the paler, bright greenish spiracular disc. Fourth instar larvae may attain a length of nearly 18 mm., just before pupation.

The pupa is characterized by the convoluted tracheal connection between the thoracic respiratory horn and the mesothoracic spiracle of the developing adult within; also by the spiracular yoke, which may sometimes lack the small apical projections, leaving the lobes broadly rounded or irregularly truncate.

Habitats of the immature stages include the mosses *Atrichum macmillani, Leucobryum glaucum, Dicranella heteromalla,* and *Mnium punctatum* and the hepatic *Calypogeia trichomanis,* all growing on sandstone cliffs. The *Leucobryum* was only about half an inch deep and was more moist than it ordinairly is in its more usual hilltop environment, where it grows in thick cushions; and the *Dicranella* was less compact than usual, probably a new growth. The commonest larval habitat of *polita cornuta* is the thin coating of *Tetraphis pellucida* moss mixed with greenish white, powdery

lichen that grows on the sheltered lower surface of outcropping rock ledges. Since water from above falls from the brink of the outcropping ledge and seepage resumes only at the contact with the ground or other rock below, this habitat is relatively dry, even at times of heavy rainfall. In contrast to this common habitat is the wet, marl-forming moss, *Gymnostomum calcareum*, from which *polita cornuta* and *johnsonella* were reared.

Notes on distribution.—ILLINOIS—La Salle County, 7 July (including a few intergrades with ssp. *pratti*); Pope County, 15 July; Vermilion County, 13 June. INDIANA—Jefferson County, 8-9 June and 3 August; Jennings County, 3 August; Montgomery County, 28 June; Owen County, 22 June, 3 and 28 August; Parke County, 23 May to 3 June, 9 to 28 June, 10 to 15 July, and 11 to 30 August. KENTUCKY—Barren County, 2 August; Edmonson County, June (?); Letcher County, 3 July (includes intergrades with ssp. *polita*); Trimble County, 3 August. MICHIGAN—Huron County, 22 July. NEW YORK—Cattaraugus County, 31 July. OHIO—Delaware County, 14 June; Geauga County, 17 July; Hocking County, 20 May to 7 June (includes two intergrades with ssp. *polita* among 101 specimens); Medina County, 4 July; Portage County, 24-25 June and 14 July (ssp. *polita* also here) and 16 August (ssp. *polita* not taken, this date); Summit County, 19 June. ONTARIO—Niagara Glen, 30 June. TENNESSEE—Fentress County, 22 July to 14 August (includes intergrades with ssp. *polita*). VIRGINIA—Giles County, 21 June to 13 July and 21 August (includes intergrades with ssp. *polita*); Wise County, 2 July (includes intergrades with ssp. *polita*). WEST VIRGINIA—Pocahontas County, 5 July (includes intergrades with ssp. *polita*); Wetzel County, 5 August.

Dolichopeza (*Oropeza*) *sayi* (Johnson)

Literature references.—*Tipula annulata* Say. Say, 1823: 25-26.

Dolichopeza annulata (Say). Osten Sacken, 1878: 40.

Oropeza annulata (Say). Needham, 1908: 210-211, pl. 16 (wing, mistakenly labelled "*Oropeza annularis*"); Pierre, 1926: 11.

Oropeza sayi Johnson (new name for *Tipula annulata* Say, preoccupied by *T. annulata* Linnaeus). Johnson, 1909: 118-119, pl. 15 (hypopygium and wing, possibly of *walleyi* Alexander, due to mixing of the two forms, as indicated below); Johnson, 1910: 708 (*walleyi*?); Alexander, 1919: 930; Alexander and McAtee, 1920: 393 (at least in part *walleyi*); Johnson, 1925: 32; Leonard, 1928: 698; Rogers, 1930: 23 (*walleyi*); Rogers, 1933: 35 and 49 (*walleyi*).

Dolichopeza (*Oropeza*) *sayi* (Johnson). Alexander, 1942: 214, fig. 26F (hypopygium); Rogers, 1942: 59; Rogers, 1949: 12; Foote, 1956: 221.

Original description.—"A dark brown stigma; abdomen pale, annulate with black. Inhabits Pennsylvania. Antennae fuscous, first and second joints whitish; rostrum, and lower portion of the front whitish; vertex and occiput dusky; palpi fuscous; thorax yellowish-brown, the indented lines paler; metathorax light livid; wings with a brown stigmata, nervures brown, arranged like those of Meigen's fig. 9, pl. 6; feet dusky-brownish; abdomen yellowish-white, incisures and their margins black, forming annulations complete. Length two-fifths of an inch."

Types.—No type specimen or series of syntypes has ever been specifically designated for this species, so far as I have been able to determine. If Say had any types, these are assumed to have been destroyed, as explained in the historical review. Needham did not clearly fix the identity of the species when he made *Tipula annulata* the type species of *Oropeza* in 1908. His illustration of the wing could apply to any species of *Oropeza*, and since his specimens, collected near Old Forge, New York, have been lost, it is impossible to say with assurance what species he actually had.

In the collection of the Museum of Comparative Zoology, beside a label reading "*O. sayi*—Johnson (*T. annulata* Say)," there are some of the twenty-five specimens that Johnson had before him when he renamed the species as *Oropeza sayi* in 1909. These are two males and two females of *Dolichopeza walleyi*. The males are those recorded (Johnson, 1909: 119) from Niagara Falls, New York, 23 June, and the females are those from Hanover, New Hampshire, 6 July 1908, and Acquia Creek, Virginia, 24 May 1896. In addition to these four, there is one male (Montpelier, Vermont, 25 June 1906) that was sent to Dr. Alexander, in trade. This specimen is the form now known as *sayi*, and it was by comparison with it that Alexander distinguished his new species, *walleyi*. The twenty specimens of Johnson's series not accounted for here were not available to me for study; possibly they are in storage in a municipal museum in Boston or in Boston University.

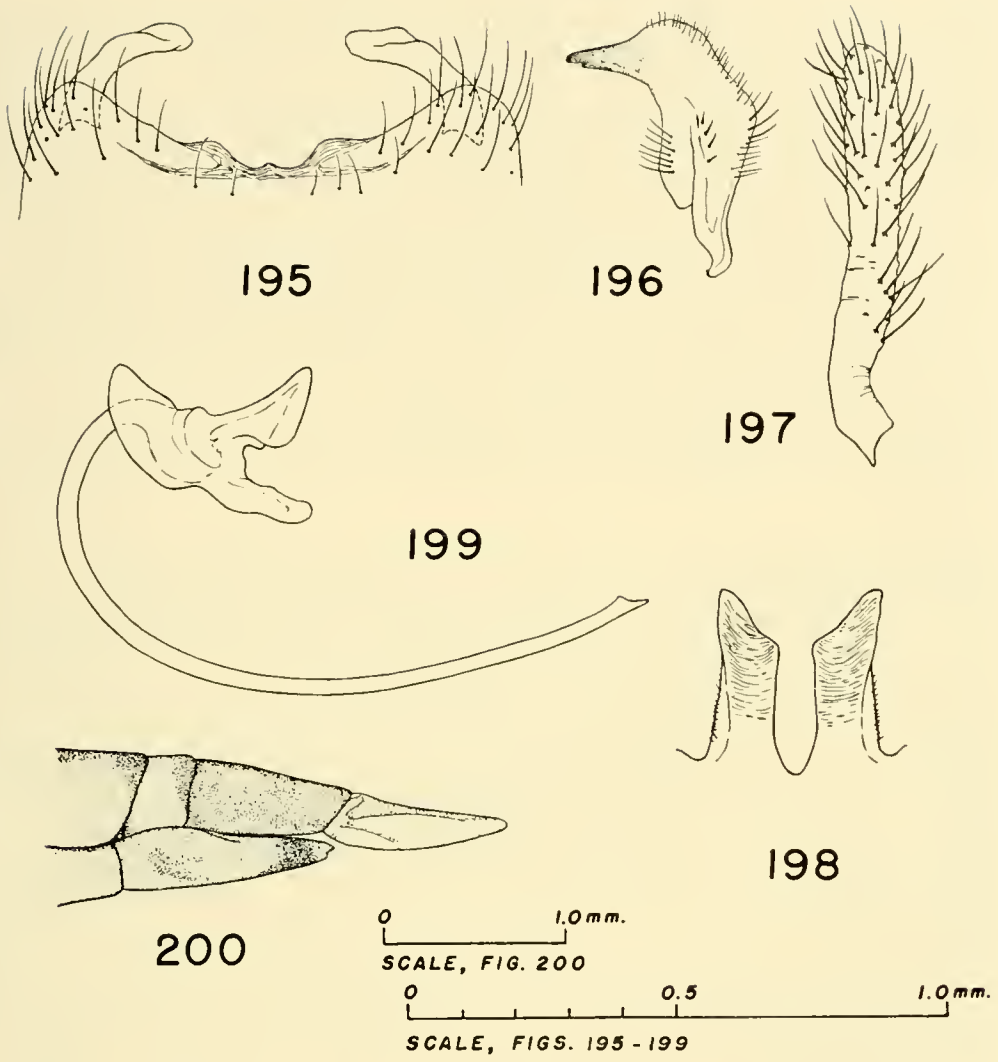
There is little in the original description of this species that is helpful in establishing its identity. Say's wording is so general as to be equally applicable to several species of *Tipula* or *Nephrotoma* that occur in Pennsylvania, as well as to certain species of *Dolichopeza*. His reference to ". . . Meigen's fig. 9, pl. 6" pertains

to a figure in the first volume of J. W. Meigen's *Systematische Beschreibung der bekannten Europäischen zweiflügeligen Insekten* (Meigen, 1818). This figure clearly represents a species of *Nephrotoma* and had been sent to Meigen under the name *Nephrotoma imperialis*; however, he placed it in *Tipula*. As pointed out in the historical review, Wiedemann identified specimens of *Dolichopeza johnsonella* and of *Tipula* as Say's *Tipula annulata*, and Osten Sacken had in his collection certain specimens he regarded as belonging to this species. Actually, Osten Sacken's specimens are one male of *Dolichopeza tridenticulata*, one male of *walleyi*, one female of *similis* (also pin-labelled "Pachyrhine?") and four females of the *obscura* group. Of these, only the male *walleyi* and the female *similis* fit at all Say's description.

This chaos of poor descriptions and lost specimens, of mixed and misidentified species, seems to me a proper occasion for designation of a neotype. Accordingly, I have selected a male specimen from New York as neotype and a female from Pennsylvania as neallotype. (At the time of this selection, I had not seen the three males of *sayi* from Luzerne County, Pennsylvania, which are in the Dietz collection in the Academy of Natural Sciences, Philadelphia; however, the neotype chosen is in better condition than any of these.) The neotype agrees with the species *Dolichopeza sayi* as distinguished from *Dolichopeza walleyi* by Alexander (1942: 214, fig. 26F) and as illustrated in my Figures 195 through 199. The neallotype agrees with my Figure 200, and both sexes conform to the descriptive comments given below. Label data on these types are as follows:

Neotype male, Ulster County (Field Catalogue Number 1), New York, 28 June 1953, G. W. Byers. Neallotype, Berks County (Field Catalogue Number 1), Pennsylvania, 15 August 1956, G. W. Byers. Locality for the neotype is Esopus Creek, 1.3 miles west of Shandaken; the specimen is in the collection of the University of Michigan Museum of Zoology. The neallotype was taken in French Creek State Park, about 11 miles southeast of Reading; the specimen is in the Snow Entomological Museum, University of Kansas.

Diagnostic characteristics.—In the field, where *sayi* often occurs together with *dorsalis*, it may be distinguished from the latter by its dark pleural markings and the much darker stigmal spot of its wing. *Dolichopeza sayi* most closely resembles *walleyi*, but the entire margin of the gonapophyses in *sayi* (Fig. 198) will readily separate males of this species from *walleyi*, in which the edges of



FIGS. 195-200. *Dolichopeza (Oropeza) sayi;* 195—ninth tergum of male, 196—left inner dististyle of male, dorsal aspect, 197—left outer dististyle, dorsal aspect, 198—gonapophyses, dorsal aspect, 199—vesica and penis, 200—terminal abdominal segments of female, left lateral aspect.

the gonapophyses are irregularly toothed. Furthermore, in the areas where these two species occur together, or where their ranges overlap, *sayi* may be recognized by the deep gray pleural spots on the mesothoracic anepisternum, ventral portion of pre-episternum and meron, for in this part of its range *walleyi* has the pleural surfaces of the thorax pale, almost as in *dorsalis*. Recognition of females is difficult, but they are separable on the basis of the color markings stated, when attention is given to their geographic locality. A further point of coloration useful is distinguishing *sayi* from *walleyi* is that the prescutal markings of the former are dark grayish brown (often approaching black in recently collected specimens), while those of *walleyi* are ordinarily a lighter reddish brown. Females of

sayi also may be easily confused with those of *similis*. In the latter, however, the abdominal annulations are brownish, are of rather uniform breadth around the body, and are about as wide as the yellowish spaces between annulations. In *sayi*, the annulations are more grayish brown, are broadest on the dorsum and taper laterally, and are often narrow or indistinct. Wing length of females of these two species overlaps in the range of 12.0 to 13.6 mm., a measurement of less than 12.0 mm. indicating the specimen is *sayi* (when other descriptive details fit, of course), and a measurement of more than 13.6 mm. indicating *similis*.

Descriptive comments.—This species may be briefly redescribed as follows:

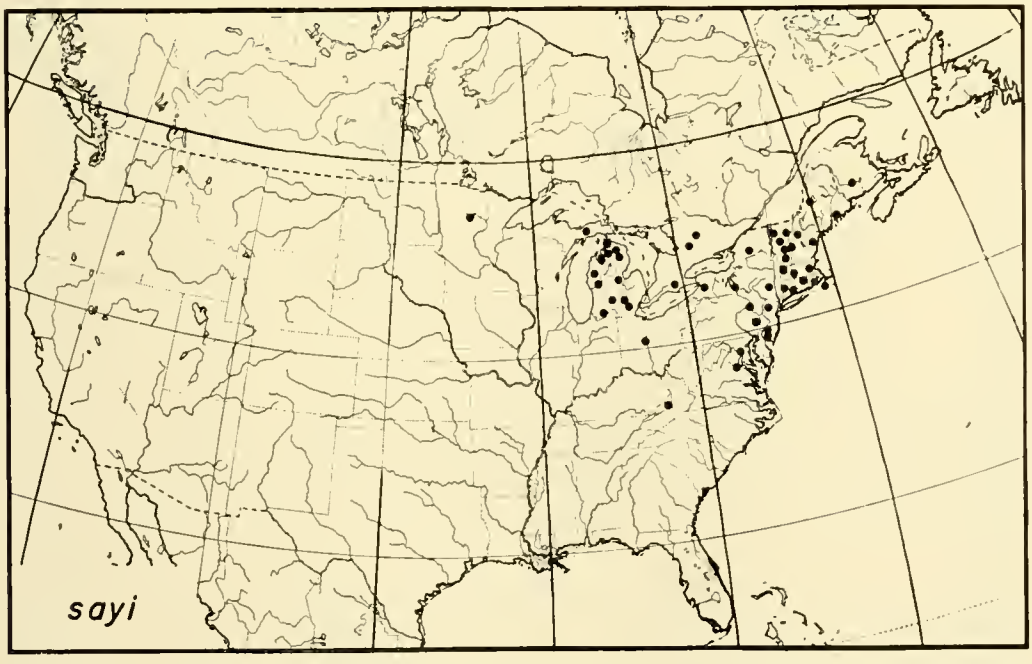
Dolichopeza sayi is in general brownish yellow, marked with dark grayish brown. Occiput gray, rostrum and frons below antennal bases yellowish; scape, pedicel and basal part of first flagellar segment yellowish, the flagellum grayish brown. Prescutum brownish yellow, marked with three longitudinal stripes of very dark grayish brown, the middle one extending farthest cephalad; scutum with two elongate, dark spots, divergent anteriorly, sometimes each divided into two; scutellum somewhat paler than prescutal ground color; mesothoracic meron and ventral part of the pre-episternum nearly as dark as prescutal stripes, anepisternum a little less darkened, the remaining thoracic pleural areas paler by contrast. Wings with a grayish tinge in living flies, the color becoming grayish amber in older specimens; stigmal spot very dark; a narrow, conspicuous band of grayish brown along the cubitus; halteres dusky. Legs dark grayish brown paling to light brown on the tarsi; coxae pale. Abdomen brownish yellow, often with the dark annulations widened dorsally, resulting in a continuous darkened stripe along the dorsal mid-line, especially in males. Annulations tapering laterally, especially on anterior segments, often incomplete and in females sometimes difficult to discern. Gonapophyses of male thick at base, flattened and slightly widened apically, the inner angle upturned, dorsal surface heavily sclerotized and a little concave, ventral surface convex, pale and sparsely pubescent (compare Figs. 7 and 198). Outer dististyles (Fig. 197) yellowish to pale yellowish brown throughout, rarely darker. Inner dististyles (Fig. 196) with an elongate, glabrous, narrowed apical portion. Ninth tergum intensely sclerotized medially, with a small central tooth flanked by two blackened lobes; tergal arms short, their distal ends only slightly expanded (Fig. 195). Female ovipositor narrowly darkened near tips of hypovalves but this area not intensely sclerotized (Fig. 200).

Body length of males varies from 8 to slightly over 10 mm. Wings of males are nearly always of greater length than the over-all body measurement, varying from about 10 to 12.5 mm. In females, on the other hand, wing length is often less even than the length of the abdomen, hence much less than over-all body length. Wing lengths of females measuring from 10 to 14 mm. ranged from 9.5 to 13 mm. Maximum expected length of wing computed from measurements of 77 females is 13.6 mm.

Venation is very constant. I have found a few instances of partial loss the the medial cross-vein, one example of a partial fusion of the subcosta with the costa, and one specimen in which the radial sector was of unusual length, suggesting that of some species of *Tipula*.

In coloration, there may be an over-all difference in intensity among specimens, so that one will appear paler in all respects than another taken at the same locality on the same date.

Apparent variation in the shape of the gonapophyses of the male may result from their partial rotation, but a few specimens have been seen in which their latero-caudal corners were rounded. The outer dististyles, though usually yellowish, occasionally have a light grayish or brownish color. A great amount of variation has been noted in the shape of the tips of the tergal arms, some suggesting those of *similis, walleyi* or *johnsonella*. As in some other species



MAP 7. Range of *Dolichopeza (Oropeza) sayi* (Johnson). Each spot represents one or more collections within a county (United States) or at a locality.

of *Dolichopeza*, it is not uncommon to find one tergal arm quite unlike the other, on one fly.

Geographical distribution.—Dolichopeza sayi is known from New Brunswick westward to northern Minnesota and southwestward to Virginia. Although it is essentially a northern species, in the character of its distribution, I would expect it to occur much more widely in Pennsylvania, Ohio and West Virginia than present records indicate. Suitable habitats for this species are also thought to occur in Canada much farther northward and westward than the now known range. Many distributional records for *sayi* published prior to 1940 will be found to apply to *walleyi*. Some of these are indicated in the literature references. In other cases, the specimens have not been seen by me.

Habitats.—Habitats in which I have collected this species are all in one way or another marshy or swampy, although in general appearance they may be quite diverse. Low, shaded vegetation of marsh borders, shrubby margins of lakes and ponds, and swampy woods are typical habitats. In the eastern part of the range, small areas of marshy terrain isolated among otherwise rocky, mesic forest lands have proved to be habitats of *sayi*. The occurrence of *sayi* in the rock gorge type of general environment, as described earlier under the natural history of adult flies, was found to be conditioned by the same microenvironmental features as those of a marsh border but present on much smaller scale. Shade sufficient to hold the temperature in the lower vegetation several degrees below that generally prevailing in the sunny parts of open marsh seems to be characteristic of *sayi* habitats. Therefore, where a pond is surrounded only by a zone of cattail (*Typha*), grasses and *Carex*, *sayi* is not likely to be found. Foote (1956: 221) reports collection of two males of *sayi* in "moist upland woods" in Delaware County, Ohio. I have not seen these specimens; the described habitat seems more appropriate for *walleyi*.

Seasonal distribution.—Where there has been enough collecting done within a limited area to give any accurate indication of the extent of the flight periods of this species, there is strong evidence of two well-marked generations per year. Rogers (1942: 59) found, in a three-year study in southern Michigan, that peaks of emergence for *sayi* came in June and August, with individuals present in May,* July and September in smaller numbers. I have

* I have been unable to verify the 1 May date given by Dr. Rogers, either by specimens or his field notes. It is not likely that *sayi* was on the wing at such an early date. Earliest established records for this area are in the last week of May.

repeated this observation in three southern Michigan localities. Evidence from the northern portion of the range suggests that only one main period of emergence, in July, is the rule. The life cycle, indicating seasons of emergence of adults, is presented in Figure 99.

Immature stages.—Eggs of an average-sized female of *Dolichopeza sayi* from southern Michigan measured .72 by .31 mm. and showed a well-developed terminal filament. The egg stage is seven days' duration, in the laboratory. Of a large number of larvae hatched, nearly all reached the first molt within two weeks, and thereafter the molts came at about one-week intervals, until the fourth instar was reached. The last instar larva very closely resembles that of *Dolichopeza walleyi* in having the ridges of microscopic hairs most pronounced on the thoracic, first, seventh and eighth abdominal segments, while the ridges are fainter on the intervening segments. Larvae just before pupation may exceed 16 mm. in length. In the laboratory, pupation did not always take place within a tube, and the six- to seven-day pupal period was, in such cases, spent with the pupa lying on its side in the bottom of the dish. At the time of emergence of the adult, however, these pupae invariably maneuvered themselves into an upright position. This was probably to prevent contact of the adult with water, for although the immature stages of *sayi* live in a semi-aquatic environment the adults are easily trapped in water and drowned. The pupa is structurally like that of *walleyi* except for details of the spiracular yoke and the absence of projections from the posterior ring of the fourth abdominal segment.

I have found the immature stages of *sayi* in wet mosses growing flat on the muddy soil in or adjacent to swamps and marsh borders. These mosses are *Amblystegium varium, Brachythecium salebrosum, Eurhynchium pulchellum* and *Hypnum lindbergii.* Larvae were also found in *Heterophyllium haldanianum* moss on a sodden, decayed log in a swamp, and in the moss *Didymodon tophaceous,* where it was growing on a rock at the bank of a brook, just below a swampy, shaded area that drained into the brook. In all cases, the larval and pupal habitat was found to be quite wet and always well shaded.

Notes on distribution.—CONNECTICUT—Litchfield County, 12-13 June; New Haven County (?), no date; Windham County, 14 June. MAINE—Cumberland County, 1 July; Hancock County, 12 July; Piscataquis County, 17 July. MARYLAND—District of Columbia (?),

29 August. MASSACHUSETTS—Berkshire County, 19 June; Dukes County, 17 July; Hampden County, 14 July; Norfolk County, 11 June and 25 August. MICHIGAN—Antrim County, 2 July; Cheboygan County, 2-3 July; Eaton County, 30 August; Lake County, 26-27 June; Livingston County, 24 May to 9 July and 28 July to 3 September; Midland County, 10 June; Montmorency County, 16 July; Newaygo County, 21 June; Oscoda County, 14 to 26 June; Otsego County, 3 July; St. Joseph County, 30 May and 12 August; Schoolcraft County, July; Washtenaw County, 5 to 17 June and 13 to 19 August. MINNESOTA—Clearwater County, 11 July. NEW BRUNSWICK—Oromocto, 9 July. NEW HAMPSHIRE—Coos County, no date; Grafton County, 6 July. NEW JERSEY—Camden County (?), 6 June; Gloucester County, 6 June; Morris County, July. NEW YORK—Erie County (?), 27 August; Herkimer County (?), August; Tompkins County (?), 6 July; Ulster County, 28 June. OHIO—Delaware County (?), 13 June. ONTARIO—Algonquin Park, 3 July and October; Gull Lake, Muskoka District, June; Simcoe, 9 June. PENNSYLVANIA—Berks County, 15 August; Luzerne County, 28 June and 8 July. VERMONT—Caledonia County, July; Chittenden County, 24 June; Washington County, 25 June; Windham County, July; Windsor County, 7 July. VIRGINIA—Stafford County (locality uncertain), 24 May; Russell County, 15 August.

Note: County records are queried when there is reason to suspect that there may be confusion of this species with *walleyi* and specimens are not available for confirmation.

Dolichopeza (*Oropeza*) *similis* (Johnson)

Literature references.—Oropeza similis Johnson. Johnson, 1909: 119, pl. 15 (hypopygium); Alexander, 1919: 930; Johnson, 1925: 32; Pierre, 1926: 12; Dickinson, 1932: 212, fig. 113 (in error; this pertains to *walleyi*).

Dolichopeza (*Oropeza*) *similis* (Johnson). Alexander, 1936; 280; Alexander, 1942: 214-215, fig. 24B (wing), fig. 26G (hypopygium); Rogers, 1942: 60, 121.

Original description.—"Head yellow, vertex brown, palpi yellow, antennae yellow becoming fuscous toward the tips. Thorax yellowish, with three wide and poorly defined black stripes covering the dorsum; scutellum, metanotum, and plurae light yellow, with livid spots between the coxae, on the plurae, and at the end of the metanotum. Abdomen yellow, with blackish rings at the margins of the segments. Genitalia brown, appendages yellow, style black

and slightly forked, appendages at base of style irregular, curved, and hamate. Ventral margin broadly emarginate. Ovipositor yellow. Halteres and legs yellow. Wings yellowish hyaline, veins and stigma dark brown. Length, male, 10 mm.; female, 13 mm."

Types.—Holotype male, Ricketts, North Mountain (Sullivan County), Pennsylvania, 8 June 1898, C. W. Johnson. Allotype, Auburndale (about 1.5 miles northwest of Newton, Middlesex County), Massachusetts, 4 June ——, C. W. Johnson. Together with the holotype and allotype in the collection of the Museum of Comparative Zoology, Harvard University, there is one female paratype. A fourth specimen mentioned by Johnson (1909: 119) is not in this collection. Although the site of the village of Ricketts, on North Mountain, is still indicated on some recent maps of Pennsylvania, the village itself has long since disappeared. Once a thriving lumbering town of several hundreds population, Ricketts vanished with the removal of all the valuable timber from the surrounding hills. Development of second-growth forest is restoring much of the area to enough of its former condition to provide many good habitats for species of *Dolichopeza.*

Diagnostic characteristics.—Although this is the largest species of North American *Dolichopeza,* it is not sufficiently larger than the similar *walleyi* or some other species occurring in the same habitats to be recognized in the field on the basis of size alone. In its natural swampland habitat, *similis* may be recognized by the combination of its large size with the golden-brown tinged wings with a dark seam along the cubitus, the yellowish body coloration and the nearly complete fusion of the prescutal stripes.

On close examination, male specimens are readily distinguishable by their unique gonapophyses (Fig. 204). In no other species is the dorsolateral angle of the gonapophysis produced into a thick, spine-like structure, projecting dorsocephalad. Also, the adminiculum is unlike that of the other species in that it bears a short spine on either side, at the apex. The female of *similis* is most likely to be confused with *sayi* and *walleyi.* Separation of these from *sayi* females is discussed in detail under that species. From *walleyi* females, these differ in having the tenth tergum more densely sclerotized than any other part of the ovipositor, the abdominal annulations of more uniform width throughout, and the prescutal stripes less distinct. Specimens of considerable age have some resemblance to females of *johnsonella* because of the indistinctness of the prescutal markings, the amber tinge of the wings and the uni-

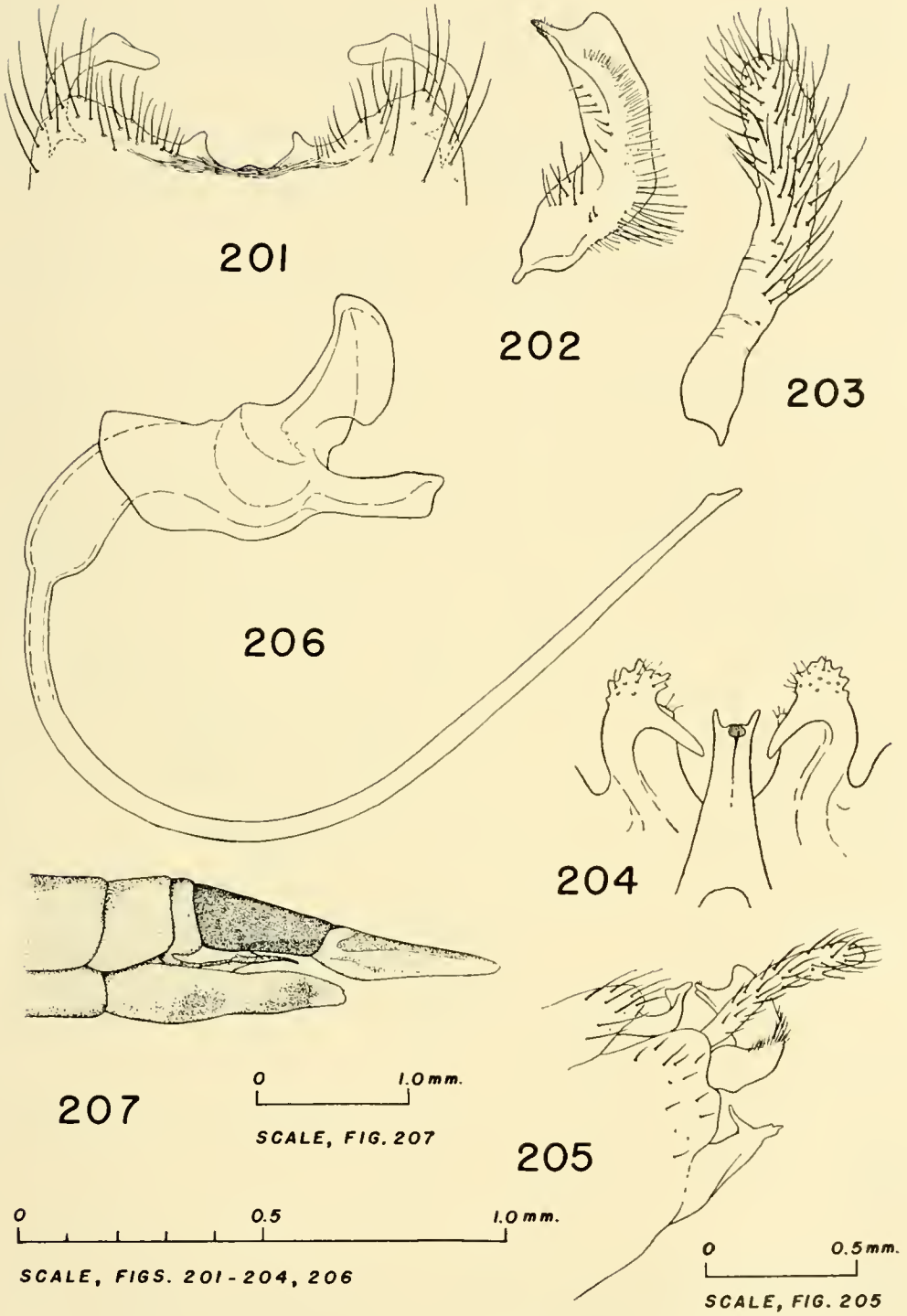
formly wide abdominal annulations; however, in *similis* females the pleural markings are more distinct, and the intense sclerotization of the hypovalve below the tenth tergum found in *johnsonella* is absent, although darkened areas somewhat like those in *carolus* females are occasionally seen (Fig. 207).

Descriptive comments.—Concerning coloration, the thoracic stripes, described by Johnson (1909: 119) as black, are a dull, reddish brown to brown, in specimens of a few years' age, grayish brown in some more recent specimens. In general aspect, *similis* has a dark, tawny-yellow color, clearly annulated on the abdomen and contrastingly marked with prescutal stripes and pleural spots on the thorax. The wings are tinged with golden brown, and the stigmal spot is long oval in most specimens.

Venation in this species is generally of the subgeneric pattern, but a few abnormalities have been seen. Presence of the veins Sc_1 and R_{1+2} was noted in a few specimens, and a spurious cross-vein in cell R_3 was equally rarely seen. The cell M_1 is occasionally nearly sessile, rarely sessile. Slight variations in position or completeness of the branches of the media are not uncommon.

Sizes recorded earlier for *similis* (Alexander, 1942: 215; Johnson, 1909: 119) seem unduly small. These measurements represent *similis* as no larger than several other species of *Oropeza*, although it is in fact the largest, so far as I can compute from the few (67) specimens I have seen. Males range from about 10 to 12 mm. in over-all body length, their wings from slightly less than 12 to about 14.5 mm. Females vary in length of body from 11 to 14.5 mm., and in wing length from 12.7 to slightly less than 15 mm. Computation of expected range of wing length (a range of three standard deviations either side of the mean of the sample) indicates the wings of females may vary from 12 to 15.6 mm.

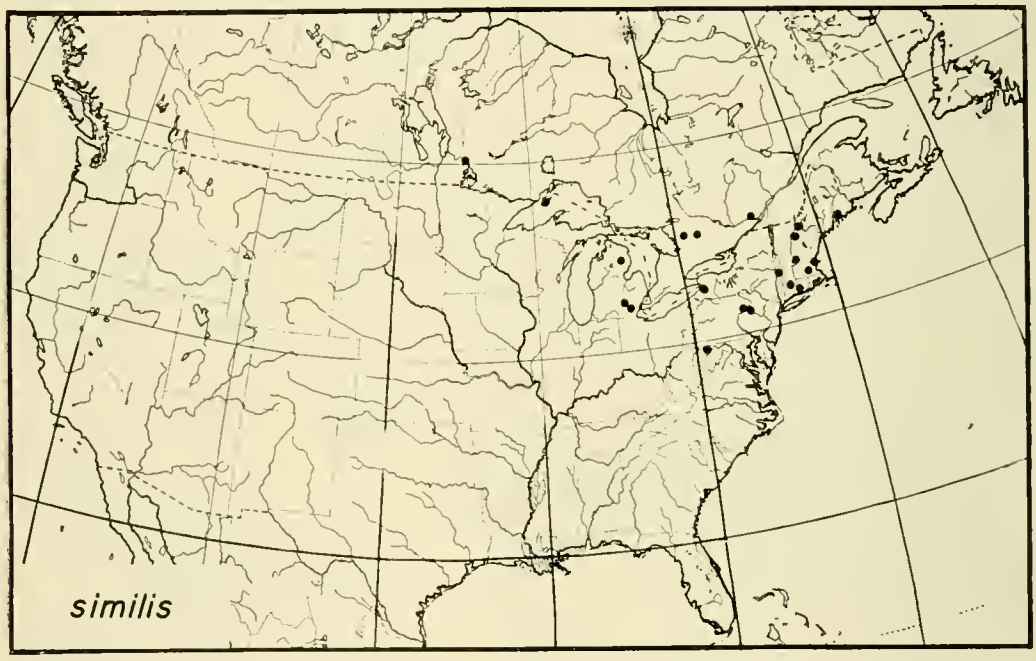
Being irregularly toothed at their margins, the gonapophyses show considerable variation, but they have been sufficiently uniform in all specimens seen to identify the species. It should be noted that these structures in males of *similis* (as also in *walleyi*, which is apparently the most closely related species) may be bent backward and downward from their normal position, in such a way that their dorsal or inner surfaces are exposed and the strong spines point caudad. While the usual profile of the ninth tergum is as shown in Figure 201, the median tooth, never very prominent, may be lacking. The inner dististyle (Fig. 202) is rather narrow throughout, with an abruptly more slender apical portion, some-



FIGS. 201-207. *Dolichopeza (Oropeza) similis;* 201—ninth tergum of male, 202—left inner dististyle of male, dorsal aspect, 203—left outer dististyle, dorsal aspect, 204—gonapophyses and adminiculum, dorsal aspect, 205—hypopygium of male, left lateral aspect, 206—vesica and penis, 207—terminal abdominal segments of female. left lateral aspect.

what suggesting the condition found in *sayi*. The basal portion of the penis is unusually enlarged (Fig. 206), more so than in *subalbipes*, the only other species in which this development has been found. This enlargement of the tube seems to be no more than a continuation of the lumen of the vesica; its particular function is unknown. One specimen has been seen in which the adminiculum bears a short, blunt spine on its ventral surface, resembling *subvenosa*, but the spine less prominent. The shape of the distal ends of the tergal arms varies a little but is usually as Figure 201.

Geographical distribution.—The range as presented by Alexander (1942:215) nineteen years ago has not been materially extended. In fact, I cannot verify his published record for north-



MAP 8. Range of *Dolichopeza (Oropeza)* similis (Johnson). Each spot represents one or more collections within a county (United States) or at a locality.

ern Indiana, and Dickinson's Wisconsin record (Dickinson, 1932: 113) is actually based on *walleyi*, so the range of *similis* is diminished to this extent. On the basis of specimens I have examined, the range extends from Maine westward to the Lake of the Woods region (Kenora District) of Ontario and southwestward to Maryland. There is a reliable record for Isle Royale, Michigan, in the Michigan collection, but the record from far western Ontario is based on a single female that I found dead in a spider web. This damaged female is darker than any other I have seen but keys to

similis without question. It seems, from knowledge of the ecological distribution of this species, that it must range much further north in the eastern part of North America and westward across Manitoba, perhaps to northern Alberta. Although the species is northern in the character of its distribution, it probably ranges much farther south in the Appalachian Mountains than present collection records indicate.

Habitats.—I have collected *similis* only a few times, always in well-shaded situations where moisture is abundant, such as a hardwoods of red maple, yellow birch and American elm, in southern Michigan. This woods is flooded every spring, remains wet or shallowly flooded until early summer and dries by late summer or early fall. Adults of *similis* were taken among ferns and other low vegetation when the water still stood three or more inches deep in most of the woods. Rogers (1942: 60, 121) took *similis* in a very similar hardwood swamp and in a tamarack-sumac swamp. He records ". . . scores of individuals . . . on the ceilings of the dimly-lit, miniature cavelike recesses that are formed where the mossy roots or root-bound platforms project over the water or the semisuspended silt margins of the swamp pools. Such low, dank recesses were sometimes shared by *obscura*, *sayi*, or *subalbipes*, but *similis* was the most abundant species here and was practically confined to these spots." Alexander (1936: 280) took *similis* along Tuckerman Trail on Mount Washington, an area much different from those already described but in which similar microhabitats may be found.

Seasonal distribution.—There is no evidence of more than one generation per year. In southern Michigan, Rogers (1942: 60, 121) made a careful study of an area where *similis* occurs, finding the flight period to be 26 May to 22 June, in the years 1936 through 1941. Late summer emergence was never found to occur. Throughout the species' range, there are date records from late May to early August, but the preponderance of specimens were taken in June. In any event, it appears that locally the flight period is quite brief, which would possibly explain the dearth of specimens in collections.

Immature stages.—The eggs of *Dolichopeza similis* are the largest of any North American species of the genus, measuring on the average .92 by .35 mm. There is no terminal filament. The first instar larvae are proportionately large, and the fourth instar

larva is the largest *Dolichopeza* larva I have found, in North America or abroad, reaching a length of 19 mm. Oddly enough, adults being hard to find, the larvae and pupae of *similis* were among the first immature stages of *Dolichopeza* encountered in this study. The larva resembles that of *walleyi* in having the minute microscopic hairs in short, definite, well-separated rows, and resembles *sayi* in the character of the dorsolateral lobes of the eighth abdominal segment. The transverse ridges of larger microscopic hairs are usually faintly indicated on the mid-region of the larva of *similis* but are a little more distinct in *walleyi*. The pupa may be recognized by the spiracular yoke, which is rather like that of *subalbipes*, and the bifid pleural spines (single-bristled in *subalbipes*).

The only known larval habitats of *similis* are the mosses *Heterophyllium haldanianum*, *Plagiothecium denticulatum* and *Tetraphis pellucida*. The *Plagiothecium* was growing on living trees, at their bases just above the water line, in a flooded hardwoods. The other mosses were growing on well decayed, wet stumps and fallen logs. All the habitats were well shaded. As they have a yellowish brown color, the large larvae are rather conspicuous in the green mosses.

Notes on distribution.—CONNECTICUT—Hartford County, 12 June; Litchfield County, 13 June. MAINE—Hancock County, 20 June. MARYLAND—Garrett County, 28 June. MASSACHUSETTS—Essex County, 12 June; Middlesex County, 4 June. MICHIGAN—Keweenaw County (Isle Royale, Lake Superior), 5 August; Livingston County, 26 May to 22 June; Oscoda County, 24 to 26 June; Washtenaw County, 5 to 22 June. NEW HAMPSHIRE—Cheshire County, 18 June; Coos County, no date; Grafton County, 2 to 8 July. NEW YORK—Erie County, 7 to 14 June and 20 August; Rensselaer County, 7 June. ONTARIO—Algonquin Park, 3 to 23 June; Burke Falls, 9 July; Kenora District (Lake of the Woods), 4 August (specimen found dead). PENNSYLVANIA—Luzerne County, 11 June; Sullivan County, 8 June. QUEBEC—Rigaud, 25 June.

Dolichopeza (*Oropeza*) *subalbipes* (Johnson)

Literature references.—*Oropeza subalbipes* Johnson. Johnson, 1909: 121-122, pl. 15 (hypopygium); Johnson, 1910: 708; Alexander, 1919: 930; Alexander and McAtee, 1920: 393; Dietz, 1921: 260; Johnson, 1925: 32; Pierre, 1926: 12; Alexander, 1928: 57; Leonard, 1928: 698; Rogers, 1930: 23; Rogers, 1933: 49.

Dolichopeza (*Oropeza*) *subalbipes* (Johnson). Alexander, 1940: 620; Alexander, 1941a: 297; Alexander, 1942: 215, fig. 26H (hypopygium); Rogers, 1942: 60, 121; Rogers, 1949: 12.

Dolichopeza subalbipes (Johnson). Judd, 1958: 624-625.

Original description.—"Similar to *O. albipes,* but readily separated by the genitalia. Tibiae more or less yellowish, tarsi entirely white. Genitalia yellow, appendages moderately long, yellow at the base, fuscous toward the tip; style yellow, appendages at the base short and tipped with small black spines, ventral margin slightly emarginate. Length, male, 9 mm.; female, 13 mm."

Types.—Holotype male, Clementon (Camden County), New Jersey, 3 June 1897, C. W. Johnson. Allotype, same locality as holotype, 8 August 1897, C. W. Johnson. Two male paratypes, those listed by Johnson from Long Branch, New Jersey, and Auburndale, Massachusetts, are together with the holotype and allotype in the collection of the Museum of Comparative Zoology, Harvard University. One male paratype (Long Branch, New Jersey) is in the Academy of Natural Sciences of Philadelphia. I have not been able to account for the other two specimens that Johnson had: the ones from Westville and Riverton, New Jersey.

Diagnostic characteristics.—Because of the appearance of the tarsi, tibiae and femora and the general coloration of the body, *subalbipes* will probably not be confused in the field with any species other than *carolus,* which is not only similarly colored but which also has the same resting posture. *Dolichopeza venosa* and *subvenosa* somewhat resemble *subalbipes* in color but lack the darkened tips on the leg segments. In differentiating *subalbipes* and *carolus* in the field, habitat is a useful but not always reliable indicator, as discussed under *carolus.*

Hypopygial structure identifies *subalbipes* males, for this is the only species of the *obscura* group in which the median region of the ninth tergum is broadly extended caudad, except *australis,* in which there is a central, pointed tooth flanked by two lower rounded lobes. The coloration of *subalbipes* is also unique in the *obscura* group. Usually, the tips of the tergal arms are bulbous and inflated (that is, hollow), a feature found in no other species of the genus. There are, however, specimens in which the tergal arms are slender, either of rather uniform thickness throughout or only slightly enlarged at the tips, often resembling those of *johnsonella* or *australis.* In *johnsonella,* the dorsal profile of the ninth tergum is

undulating (Fig. 157), while in *subalbipes* (Figs. 208, 209) and *australis* (Fig. 137) there is a definitely projecting, broad extension or lobe.

Females of *subalbipes* may be distinguished from those of *carolus* by their lacking the darkly sclerotized spot, near the base of each hypovalve, characteristic of the latter species. In *subalbipes*, also, there is a greater contrast between the dark mesothoracic anepisternum and the pale dorsal portion of the pre-episternum than is found in *carolus*.

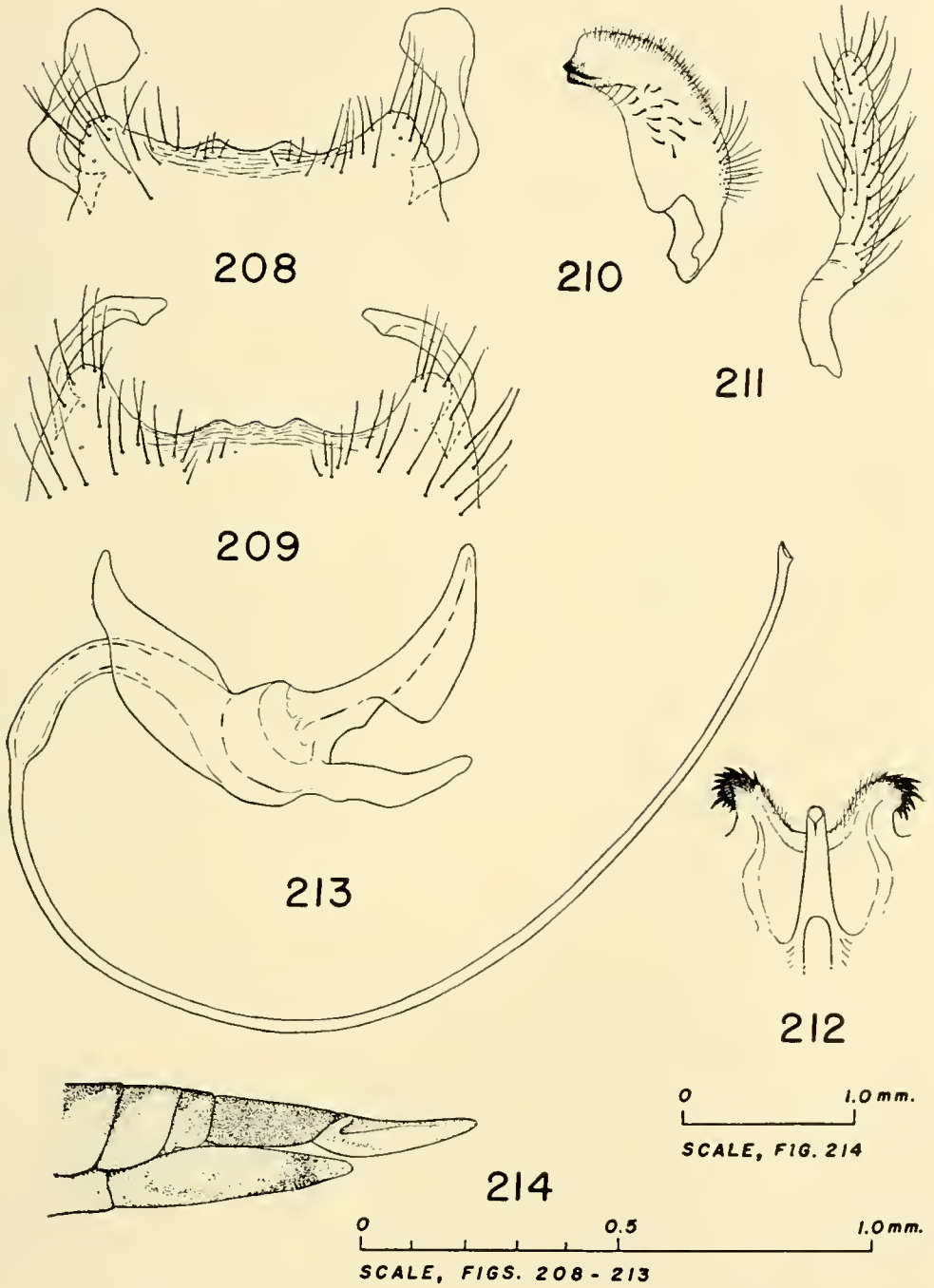
Descriptive comments.—The close similarity of color detail between *subalbipes* and *carolus* is covered in the discussion of the latter species. It might be added that both species have, in general, the same range of variation in coloration, except that there appears to me to be a tendency in northern populations of *subalbipes* to have the darker areas of the body (prescutal stripes, pleural spots, abdominal annulations, etc.) relatively darker than the corresponding areas on individuals of *carolus* from the same locality. For example, where both species were collected together in Wisconsin, *carolus* was the paler in over-all appearance.

Locally the incidence of venational variation is very high, and, as in other species of the *obscura* group especially, this variation is concentrated in the branches of the media. In a Florida population, several specimens had a short vein projecting into the cell M_2 from the medial cross-vein; and in a population from southern Georgia there was an unusual amount of fragmentation of the distal ends of the branches of the media. These and an extraordinary variation in a specimen from Alabama are illustrated in Figures 49-51.

Size variation in *Dolichopeza subalbipes* is not conspicuous through most of the range, an average male of the spring generation measuring about 9.5 mm. in body length, with an 11.5 mm. wing. Late summer males are ordinarily slightly smaller in all dimensions than those of the spring period of emergence. However, I have seen a few males from northern peninsular Florida, all collected between late October and early March, that are remarkably diminutive, the smallest having a body length of only 7 mm. and a wing length of 7.5 mm. Another very small male, like these, is from southern Georgia but was taken on the tenth of June. These males all differ structurally from most *subalbipes* of the area, as described below. Largest males seen were from Michigan and from the Appalachian Mountains in Giles County, Virginia. These flies reach a body length of slightly over 10 mm., their wings around

12 mm. Females attain greater lengths (11.2 to 15 mm.), and their wings are nearly always shorter than the over-all body length (10 to 12.5 mm.).

The most outstanding variation noted in this species is that of the hypopygium of the male, particularly of the shape of the tergal



FIGS. 208-214. *Dolichopeza (Oropeza) subalbipes;* 208—ninth tergum of male, showing expanded tergal arms, 209—ninth tergum of male with slender tergal arms, 210—left inner dististyle of male, dorsal aspect, 211—left outer dististyle, dorsal aspect, 212—gonapophyses and adminiculum, dorsal aspect, 213—vesica and penis, 214—terminal abdominal segments of female, left lateral aspect.

arm, as discussed earlier in the section on intraspecific variation. One form has tergal arms the tips of which are bulbous and knob-like (Fig. 208). The holotype of *subalbipes* belongs to this form. In Florida, the type of tergal arm with bulbous or inflated tip is by far the most common, and all specimens having the slender-tipped tergal arm are the small, winter males mentioned above. Small samples of *subalbipes* from Clearwater County, Minnesota, Juneau County, Wisconsin, and Washtenaw County, Michigan, contain males having only the type of tergal arm that is of rather uniform width or thickness throughout (Fig. 209; and Alexander, 1942: 213, fig. 26H). A sample of 15 males from Livingston County, Michigan, contained seven with the inflated tip and eight with the slender tip, with an indication that the slender tip form is somewhat more abundant in the spring generation. In Cheboygan County, Michigan (northern Lower Peninsula), Giles County, Virginia, and Fentress County, Tennessee, areas from which large samples of *subalbipes* are available, both types of tergal arm are found, the slender type commoner in the more northern localities. Very few specimens that could possibly be regarded as intergrades have been seen, an example being a fly from eastern Tennessee in which the tergal arms have inflated tips but are reduced in over-all size.

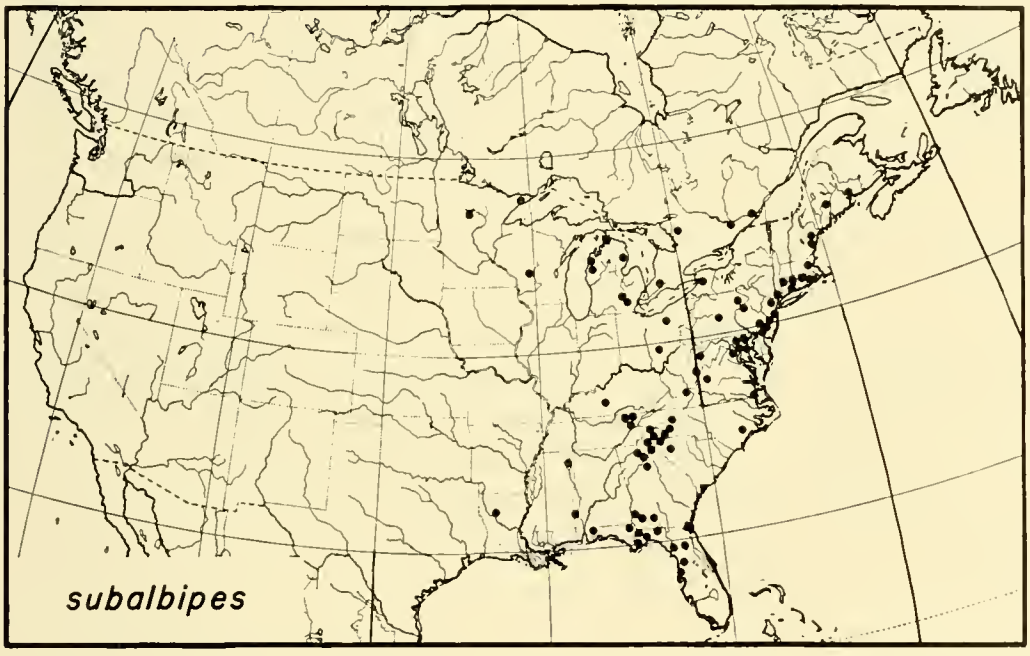
Less conspicuous but much more variable in shape is the broad, projecting median lobe of the ninth tergum. This structure may bear three obtuse peaks or, less often, two; it may project only slightly or may extend well caudad from the adjacent margin of the tergum; and it may be relatively either wide or narrow. Two commonly observed profiles of the ninth tergum are illustrated in Figures 208 and 209.

In certain specimens there is, as in *Dolichopeza similis*, a basal enlargement of the penis, although in *subalbipes* this is of a smaller diameter and somewhat greater length (Fig. 213). This character has been examined in only a few specimens that were dissected or cleared and mounted on microscope slides, but among these perhaps two dozen males there was close correlation between the presence of the basal enlargement of the penis and the inflated tip of the tergal arm. In males having tergal arms with slender tips, the penis is thick at the base but not more than twice its diameter at mid-length and without the abrupt reduction in diameter shown in Figure 213.

The descriptive data just presented lead one to question whether the nominal species *subalbipes* is not in reality two species. The two forms of males seem to exist together throughout the range, and

I have so far been unable to distinguish any two corresponding types of females. Variation in the shape of the ninth tergum of males cuts across the line drawn on the basis of the tergal arm and the basal enlargement of the penis, as does variation in the shape of the inner dististyle (which is sometimes wider near its apex than illustrated in Figure 210). In view of these things, I regard the described differences between males as polymorphic forms within one species.

Geographical distribution.—Dolichopeza subalbipes ranges farther southwest than any other species, as far as is now known, one specimen having been collected in Natchitoches County, Louisiana.



MAP 9. Range of *Dolichopeza (Oropeza) subalbipes* (Johnson). Each spot represents one or more collections within a county (United States) or at a locality.

I have not seen this fly, a female, which was reported to me as *carolus*, but I feel confident that it is not that species, and it seems unlikely that it would have been confused with any species other than *subalbipes*. Alexander (1942: 215) has also regarded this record as *subalbipes*. He reports the species from Indiana, which I am unable to verify by specimens or collection records, although I have no doubt it occurs there. The range of *Dolichopeza subalbipes* extends from New Brunswick westward to northern Minnesota and southward as far as central Florida and the Gulf Coastal Plain as far west as Louisiana. I believe there are suitable habitats in Kentucky, Indiana, Illinois, eastern Arkansas, western Tennessee

and eastern Texas. Also, the natural range probably extends much farther north and northwestward than records now available indicate.

Habitats.—Adults of *Dolichopeza subalbipes* have nearly always been taken in close association with low, leafy vegetation of swampy or marshy places, or along shaded streams. It was mentioned earlier that *subalbipes* had been collected in a rocky ravine, in Wisconsin. This was an unusual locality (Rocky Arbor State Park), however, in that while rock gorge habitats could be found along its sandstone walls, the flat floor, some 200 yards in width, was covered with a typical northern swamp. Only once, in Portage County, Ohio, have I taken this species in a rocky ravine type of general habitat where even localized swampy conditions were absent altogether. In Minnesota and northern Michigan, *subalbipes* was taken in cool, well-shaded, swampy lowlands; in southern Michigan, the habitats where I found this species were swampy hardwoods and the seasonally flooded hardwood zone around a bog. I have netted *subalbipes* among dense ferns and deep grasses along forest brooks, in the Appalachian Mountains from northern Georgia to Maine, and in *Sphagnum* bogs (where other mosses also were abundant) in West Virginia and Michigan. On the Cumberland Plateau of eastern Tennessee, Rogers (1930: 23) found *subalbipes* "more confined to the upland" than *carolus* and "taken from the stream-margin thickets, sphagnum-huckleberry bogs, and from the banks of both cleared and wooded brooks. A few records are from the talus slope brooks and from the river bank of Clear Fork, but it was not collected from the 'rock houses' or the base of the wet rim rock." In Pennsylvania, Dietz (1921: 260) observed *subalbipes* to be an inhabitant of "swampy places." Northern Florida habitats of this species are described as ". . . beneath luxuriant ferns and herbage that overhang wooded rills and small brooks" (Rogers, 1933: 49). All habitats described by other authors are places in which damp mosses are likely to have been growing.

Seasonal distribution.—There is evidence of rather continuous emergence of adults, through most of the year, in the Florida region. North of Florida, however, the indication is that two annual generations occur, except in the northernmost parts of the United States and in Canada, where collection records are so few as to render the situation obscure. There are far northern records for June through August, but most of these are for July and suggest a single, midsummer generation for this region. Rogers (1942: 60, 121) found

the adults of *subalbipes* on the wing in southern Michigan from 2 June to 14 July and from 14 to 28 August, the June generation the largest in numbers. He records the species as "abundant in the birch-maple swamp on June 5, and spread for 150 feet or more into the adjacent oak-hickory woods. . . . Apparently a huge 'hatch' had taken place on June 3, 4, or 5, for only a few teneral males could be found in the swamp on June 3." In eastern Tennessee, another region in which *subalbipes* has been collected extensively enough to indicate its seasonal distribution, Rogers (1930: 23) found it in May to early July and again in August.

Immature stages.—Eggs of an average sized female of *Dolichopeza subalbipes* from southern Michigan measured .83 by .36 mm., and those of a small female from Florida (one taken in February with the small males noted above) averaged only about .72 by .34 mm. In each case, the number of eggs matured appears to be around 100. There is no indication of a terminal filament. Larvae of the first two instars are not known, but the third instar very closely resembles the fourth. The fourth instar larva is one of the easiest to identify of all species of *Oropeza.* The larger microscopic hairs on the dorsum of all segments are longer than in any other species except *venosa* and are arranged in broken and irregular transverse ridges, again as in *venosa.* The minute microscopic hairs are in long, indefinite rows or sometimes not arranged in rows, while in *venosa* they are in shorter, well-defined rows.

Larval habitats are only poorly known. Rogers (1933: 49) found the larvae in "saturated mosses and liverworts, on wet earth banks, on rocks and (more rarely) sodden logs." He observed that they fed on the growing portion of the habitat plants, mainly at night. His collection of these larvae was found in include both *obscura* and *subalbipes,* however, and the bryophytes were not identified. My few collections of the larvae and pupae of *subalbipes,* made in southern Michigan, were from the mosses *Tetraphis pellucida* and *Dicranum scoparium* and the hepatic, *Geocalyx graveolens.* These bryophytes were all found on extremely decomposed and sodden wood, in a birch-maple-elm swamp, but the plants themselves were not saturated with water, as were those described by Rogers. I have never found *subalbipes* larvae in mosses as wet as those in which the immatures of *sayi* or *dorsalis* occur. Accordingly, I question the inference by Judd (1958: 624 ff.) that *subalbipes* adults emerged from water about two feet deep. It is possible that larvae were in some fragment of moss accidentally

adhered to his tent trap at or above the water line, but that they might have been in submerged mosses seems unlikely to me, inasmuch as my laboratory experiments indicate the larvae of *Dolichopeza* spp. drown when wholly covered with water.

The pupa of *subalbipes* may be recognized by its slender lobed spiracular yoke and the fact that the pleural spinous processes are tipped each by a single bristle. Color comparison of the pupa of this species with that of *obscura* is made in the discussion of the pupa of the latter. The pupal stadium lasts six or seven days, under laboratory conditions.

Notes on distribution.—ALABAMA—Washington County, 14 June. CONNECTICUT—Hartford County, 14 June; Litchfield County, 31 May; New Haven County, no date; Windham County, 14-15 June. FLORIDA—Alachua County, 16 January, 17 to 28 February, 11 to 21 March, 1 to 16 April, 3 June, 25 July, 14 October, and 12 to 25 November; Escambia County, 7 April; Gadsden County, 28 to 31 March and 5 June; Hernando County, 21 March; Jackson County, 31 March to 29 April; Jefferson County, 31 March; Leon County, 18 March and 31 March to 13 June; Liberty County, 3 March to 26 April, and 15 to 27 July; Marion County, 4 April; Nassau County, 27 April; Putnam County, records for every month except December and February, with peak abundance in June (23 date records). GEORGIA—Baker County, 27 January, 9 to 24 February, 24 to 31 March, 7 and 21 April, 26 May, 27 August, and 14 October; Clay County, July; Cook County, 10 June; Hall County, 6 June; Lumpkin County, 2 to 8 June; Rabun County, 12 June; Union County, 23 May and 10 and 28 June. KENTUCKY—Edmonson County, June (?). LOUISIANA—Natchitoches County, no date. MAINE—Cumberland County, 1 July; Penobscot County, 18 June; York County, 1 July. MARYLAND—District of Columbia, 29 August; Anne Arundel County, 20 June; Baltimore County, 17 June; Prince George's County, 9 June. MASSACHUSETTS—Middlesex County, 10 to 16 June. MICHIGAN—Cheboygan County, 3 and 31 July; Iosco County, 22 July; Lake County, 27 June; Livingston County, 2 June to 8 (14?) July and 14 to 28 August; Manistee County, 21 June; Washtenaw County, 12 and 20 June. MINNESOTA—Clearwater County, 11 July; Cook County, 5 July. MISSISSIPPI—Itawamba County, 14 July. NEW BRUNSWICK—Charlotte County, 5 July. NEW JERSEY—Bergen County, 1 to 15 June; Burlington County, 11 August; Camden County, 3 June and 8 August; Gloucester County, 6 June; Monmouth County, 12 June. NEW YORK—Erie County, 9 July; West-

chester County, 9 June. NORTH CAROLINA—Buncombe County, 12 June; Macon County, 11 to 13 June and 26 August to 4 September; Mitchell County, 16 June; Onslow County, 9 July; Swain County, 20 June; Transylvania County, 8-9 June; Yancey County, 7 June. OHIO—Hocking County, 6 June; Portage County, 25 June. ONTARIO—Blackburn (5 miles east of Ottawa), 6 August; Kearney (about 20 miles west of Algonquin Park), 2 July; Byron (4 miles west of London), 16 June. PENNSYLVANIA—Berks County, 15 August; Centre County, 25-26 June and 4 to 9 July; Luzerne County, 4 and 14 to 19 June; Sullivan County, 10 July. QUEBEC—Montreal, 14 July. RHODE ISLAND—Kent County, 15 to 21 June. SOUTH CAROLINA—Greenville County, 22 May to 7 June and 20 July to 11 August. TENNESSEE—Fentress County, 6 to 18 June, 5 to 9 July, and 8 to 13 August; Morgan County, 12 June; Scott County, 29-30 May; Sevier County, 15 and 30 June. VIRGINIA—Arlington County, 31 May; Augusta County, 28 June; Giles County, 31 May to 24 June; Norfolk County, 10 August. WEST VIRGINIA—Pocahontas County, 23 June and 5 July; Tucker County, 24 June. WISCONSIN—Juneau County, 6 July.

Dolichopeza (*Oropeza*) *subvenosa* Alexander

Literature references.—Dolichopeza (*Oropeza*) *subvenosa* Alexander. Alexander, 1940: 618-620, fig. 15 (wing), fig 18 (hypopygium); Alexander, 1941a: 297.

Original description.—"Allied to *venosa;* mesonotal praescutum grayish yellow with three conspicuous blackish stripes; pleura grayish yellow, variegated with brown; tips of tibiae and the tarsi paling to yellow, femoral tips narrowly brightened; wings with a strong brownish tinge; stigma darker brown, with conspicuous cream-colored post-stigmal areas; male hypopygium with the inner dististyle broad, especially opposite its outer end; aedeagus with a strong spine on ventral face near apex. Male. Length, about 9-11 mm.; wing, 11-12.5 mm.; antenna, about 3-3.5 mm. Female. Length, about 11 mm.; wing, 11 mm.

"Frontal prolongation of head pale testaceous; palpi brown. Antennae with scape and pedicel pale yellow; base of first flagellar segment pale, the remainder black; segments relatively long, subcylindrical, much exceeding the erect verticils; pubescence of segments short. Head brownish gray, darker in central portion.

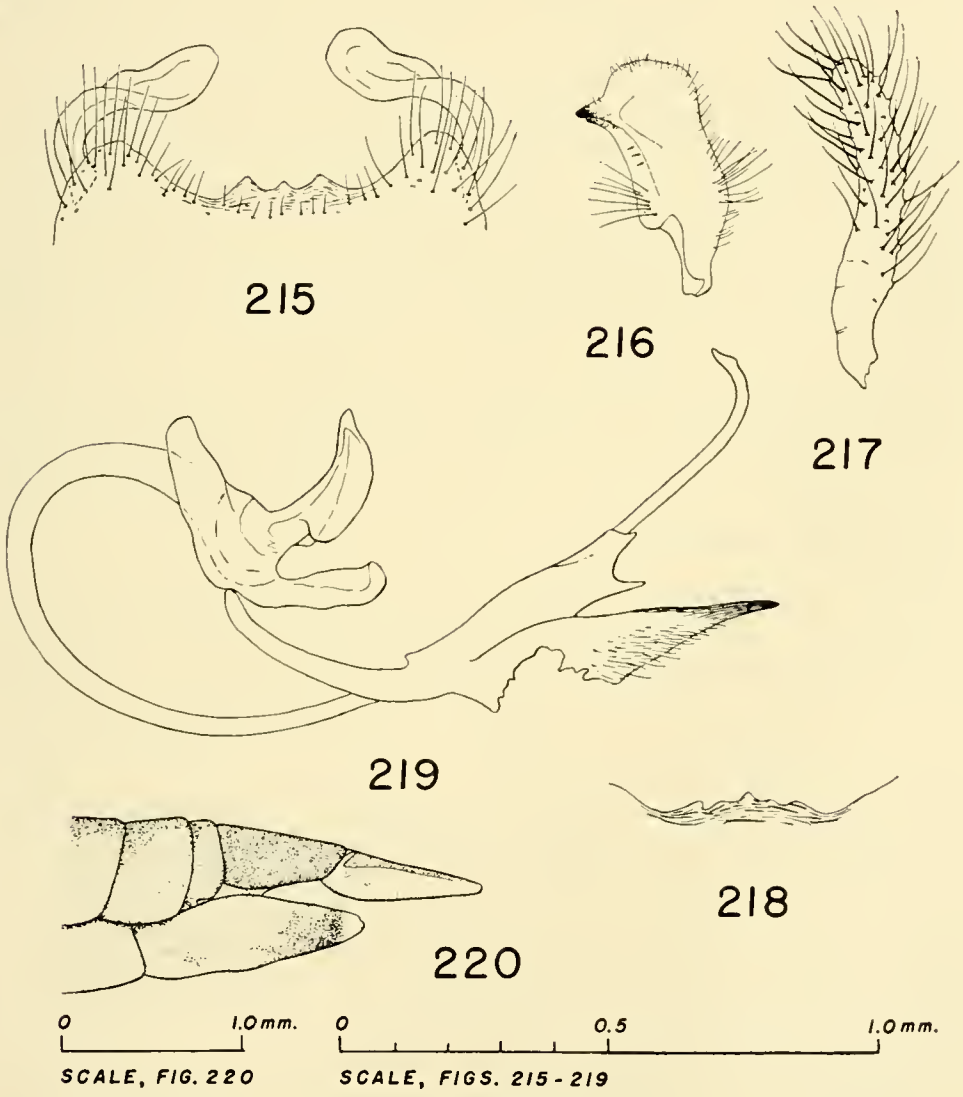
"Pronotum brown, blackened medially. Mesonotal praescutum grayish yellow, with three conspicuous blackish stripes, the posterior interspaces obscured; scutal lobes brownish black, the median

area very restrictedly paler; posterior sclerites not black or brownish black. Pleura grayish yellow, variegated with brown on the anepisternum, ventral sternopleurite, meron and extreme ventral edge of pleurotergite. Halteres elongate, stem yellow, knob darkened. Legs with coxae pale, the fore pair darker; trochanters yellow; femora blackened, the tips narrowly pale; tibiae dark brown, paling to obscure yellow on distal portion; tarsi obscure yellow. Wings with a strong brownish tinge; stigma oval, dark brown; a conspicuous, paler brown seam along vein Cu; membrane adjoining the stigma, especially in cells beyond the stigma, cream-yellow; a restricted brightening across the fork of M; veins brown. Venation: Sc_2 ending opposite or just beyond origin of Rs.

"Abdominal segments blackened medially and on basal rings of segments, leaving extensive yellow areas on sides of posterior rings; outer sternites and tergites, including hypopygium, more uniformly blackened. Male hypopygium with the lateral arms of tergite blackened, the apices dilated into oval spatulate blades, the margins smooth or without conspicuous angulations; median area of tergite trilobed, the central lobe longer and more spinous. Outer dististyle uniformly blackened, cylindrical, a little exceeding the inner style. Inner dististyle much deeper than in *venosa*, elevated just above the short apical beak. Gonapophyses much as in *venosa*, appearing as blackened spines, their bases with conspicuous setae. Aedeagus close to apex on ventral face with a strong, erect spine, this variable in length but always strongly developed. In *venosa*, the lateral arms of tergite are more angular, the median area of the caudal margin with the central lobe low or lacking; inner dististyle narrower, especially above and before the apical beak; aedeagus without spine."

Types.—Holotype male, Anakeesta Ridge, 4500 ft. (Great Smoky Mountains National Park), Tennessee, 12 June 1939, C. P. Alexander. Allotype, same locality as holotype, 4000 ft., 5 June 1939, C. P. Alexander. Eight male paratypes, of which six are from the Great Smoky Mountains National Park, all above 2500 feet elevation, various dates in June and various collectors; the other two from nearby Mt. Mitchell, Yancey County, North Carolina, above 4000 feet, June, collected by C. P. Alexander. Holotype, allotype and five paratypes are in the collection of Dr. Alexander, at Amherst, Massachusetts. One paratype is in the collection of the University of Michigan Museum of Zoology, and one is in the United States National Museum.

Diagnostic characteristics.—Dolichopeza subvenosa is differentiated from *carolus* and *subalbipes* by its over-all darker color, by having yellowish instead of white tarsi, and by lacking the contrastingly darkened tips on the femora and tibiae. It very closely resembles the more northern *Dolichopeza venosa,* and I have not yet discovered any reliable means of distinguishing the females of the two forms. The most readily visible characters for recognition of males of *subvenosa* from those of *venosa* are the presence of a conspicuous spine on the ventral or posterior surface of the adminiculum (aedeagus, in Alexander's terminology) and the more



FIGS. 215-220. *Dolichopeza (Oropeza) subvenosa;* 215—ninth tergum of male, 216—left inner dististyle of male, dorsal aspect, 217—left outer dististyle, dorsal aspect, 218—medio-posterior margin of ninth tergum of male holotype, 219—vesica, penis, adminiculum, adminicular rod and gonapophysis, left lateral aspect, 220—terminal abdominal segments of female, left lateral aspect.

rounded tips of the lateral arms of the ninth tergum (Figs. 219, 215). Although the greater subapical width of the inner dististyle in *subvenosa* is a good indication of the species (as compared to *venosa*), it is not easy to observe except in alcoholic material or specimens mounted on microscopic slides, as the tips of these structures are usually more or less drawn down into the genital chamber.

Descriptive comments.—A tawny-yellow fly with dark brown markings, *subvenosa* is slightly paler in average, over-all coloration than *venosa*, partly by reason of the narrower abdominal annulations and partly because of the less intense color of these and the other markings. A few specimens from Giles County, Virginia, have darker tarsi than usual, these being light brown to the tips.

Wing venation in the relatively small number of specimens examined (138) was found to adhere closely to the subgeneric pattern. Slight variations in the medial field, such as the intersection of the m-cu cross-vein with the short M_{3+4} or with M_4 beyond its junction with M_3 are not uncommon. One male was seen in which the discal cell was closed distally by a temporary fusion of M_3 and M_{1+2}, in the absence of the medial cross-vein.

Body size of males ranges from 9 to nearly 11.5 mm., with the wings varying from 10.5 to 13 mm. Females are slightly larger, their over-all body length being from 11 to 12.5 mm. and their wings from 11 to 13 mm.

There is so much variation in the male hypopygial structures used in differentiating *subvenosa* and *venosa* that for a time I regarded these two forms as only subspecifically distinct. The spine on the adminiculum, for example, which is the most outstanding feature of *subvenosa*, is normally long, acute and conspicuous, as in Figure 219; however, there are occasional specimens in which it is reduced to a low, obtuse bump, even less conspicuous than the spinous development found on the adminiculum in many specimens of *venosa*. The more rounded edges of the flattened, apical portion of the tergal arm are an ordinarily reliable means of recognition of *subvenosa*, but this character also varies across the boundary between species. Males with angularly spatulate tergal arms but otherwise typically *subvenosa* have been seen from Virginia and North Carolina, while the rounded form has been observed in *venosa* males from New York and Michigan. A more detailed analysis of variation in hypopygial structures will be found in the discussion of *Dolichopeza venosa*. The intensely sclerotized,

sharply pointed gonapophyses and darkly colored outer dististyles appear to me to be the same in both species. The pronounced hump in the outer curvature of the inner dististyle just before the short apical prolongation (Fig. 216) is a character of *subvenosa* that is only very rarely seen in *venosa,* the inner dististyle in the latter species ordinarily being much more slender near the tip (Fig. 231).

Geographical distribution.—For eighteen years following its description, *subvenosa* was known only from the central Appalachian Mountains of Tennessee, North Carolina, and nearby Georgia and South Carolina. Dr. Rogers collected many specimens also in southwestern Virginia, but the range of the species remained widely separated from the known range of *venosa,* to the north. Records of *venosa* in South Carolina (Alexander, 1942: 215) pertain to this form. Intensive collecting in West Virginia, southern Ohio and Pennsylvania and western Virginia in 1958 did much to clarify the respective ranges of *subvenosa* and *venosa,* the gap between the two finally being closed in Preston County, northern West Virginia, and subsequently in Garrett County, western Maryland, with the discovery of the presence of both forms, there. These ranges, so far wholly allopatric, are conveniently mapped together, the distribution map included with the discussion of *venosa.* As mentioned earlier, I had considered *subvenosa* and *venosa* subspecies of one species, at one time; however, because there is no clear zone of intergradation between the two and because their identifying characteristics are sufficient to distinguish the average specimen (on the basis of males), I have abandoned that opinion and recognize two species.

Habitats.—Most collection records for *subvenosa* are for high elevations in the Appalachians, such as the 2500 to 4500 foot elevations of the type series. I have taken the species at elevations near 1000 feet, which is approximately that of the Greenville, South Carolina, locality, and at various elevations up to around 6600 feet, near the summit of Mt. Mitchell, Yancey County, North Carolina. The species thus has a considerable vertical distribution, yet not as great as either *obscura* or *americana,* species I took together with it atop Mt. Mitchell. Within its mountainous and forested range, *subvenosa* has diurnal resting places similar to those of *venosa*: shaded, rocky crevices, undercut earthen banks, and other situations where deep shade obtains. Occasionally I found *subvenosa* suspended from ferns or other leafy vegetation near such darkened

crannies. Along mountain brooks, they are often found very near the water, such as beneath an overhanging, rootbound and mossy bank, where the clearance above the water may be only a few inches. Unpublished field notes by Dr. Rogers indicate similar habitats in the places where he collected, near Mountain Lake, Virginia, and at various localities in North Carolina.

Seasonal distribution.—All but a few of the records for this species are in June, suggesting that there is but one generation per year, and the numbers of individuals taken on the various dates indicate the peak of emergence in the southern and central Appalachian Mountains comes about the end of the first week of June, perhaps a week later than that in West Virginia. At no time or place, however, have I obtained *subvenosa* in large numbers—never in aggregations and never more numerous than any other species of *Dolichopeza* occurring together with it.

Immature stages.—No study has been made of the immature stages of this species. Eggs dissected from the abdomen of a female of average size were found to have nearly the same measurements as those of *venosa*. The average dimensions were .79 by .34 mm., but eggs from a slightly smaller female measured only .75 by .31 mm. There is no terminal filament. No larvae have been found, but I would expect them to resemble rather closely those of *venosa*. Pupal skins apparently of this species were collected from a sparse growth of *Mnium* sp. on a steep soil bank above a mountain brook in western North Carolina. In these, the spiracular yoke resembles that of *venosa* except that the outer secondary lobes are more developed; also, the reticulation of the mesonotum is faint, consisting mostly of transverse wrinkles similar to those along the mid-line. There are spinous processes on the fourth abdominal sternum about half as long as those on the fifth. Four female pupae from North Carolina and Georgia ranged in size from 10.2 to 12.0 mm.; males assignable to this species were not found.

Notes on distribution.—GEORGIA—Rabun County, 5 June; Towns County, 12 June; Union County, 10 June. MARYLAND—Garrett County, 28 June (*venosa* also here). NORTH CAROLINA—Burke County, 14 June; Haywood County, 28 May; Macon County, 8 to 15 June; Swain County, 11 to 17 and 30 June; Transylvania County, 9 June; Yancey County, 7 to 22 June. SOUTH CAROLINA—Greenville County, 3 to 29 June. TENNESSEE—Sevier County, 12 to 19 and 30 June. VIRGINIA—Giles County, 8 June to 9 July. WEST VIRGINIA—

Pendleton County, 27 June; Preston County, 25 June (*venosa* also here); Tucker County, 24-25 June.

Dolichopeza (*Oropeza*) *tridenticulata* Alexander

Literature references.—*Dolichopeza* (*Oropeza*) *tridenticulata* Alexander. Alexander, 1931c: 177-178; Alexander, 1940: 620; Alexander, 1941a: 297; Alexander, 1942: 215, fig. 26I (hypopygium); Foote, 1956: 222.

As *Oropeza obscura* Johnson. Johnson, 1909: 122 (part), pl. 15 (wing); Rogers, 1930: 22-23 (part); Dickinson, 1932: 212 (part), fig. 114 (wing).

Dolichopeza (*Oropeza*) *tridentata* Alexander. Crampton, 1942: 147, fig. 6A (misspelling).

Original description.—"Male. Length about 10 mm.; wing 11 mm. Described from alcoholic specimens. Closely related to *obscura,* differing especially in the structure of the male hypopygium. Antennae dark brown. Mesonotum dark reddish brown, the pleura still darker. Legs with the tarsi a little paler than the tibiae. Wings suffused with brown, the oval stigma slightly darker brown; paler areas before and beyond the stigma and across the base of cell 1st M_2. Abdominal segments brownish yellow, conspicuously ringed with dark brown on the incisures, on the sternites the bases of the segments more broadly darkened than the apices. Male hypopygium with the central portion of the tergal margin produced into a small rectangular area that bears three small chitinized points; lateral arms of tergite evenly rounded at tips. Inner dististyle very broad, weakly bidentate at tip, one of the points being a small blackened spine. Outer dististyle and gonapophyses much as in *obscura.*"

Types.—Holotype male, Goshen, Hampshire County, Massachusetts, 1 July 1931, G. C. Crampton. The holotype, from alcohol, is in the collection of Dr. C. P. Alexander, at Amherst, Massachusetts. Several females taken at the same time as the holotype were not designated paratypes and have apparently been discarded.

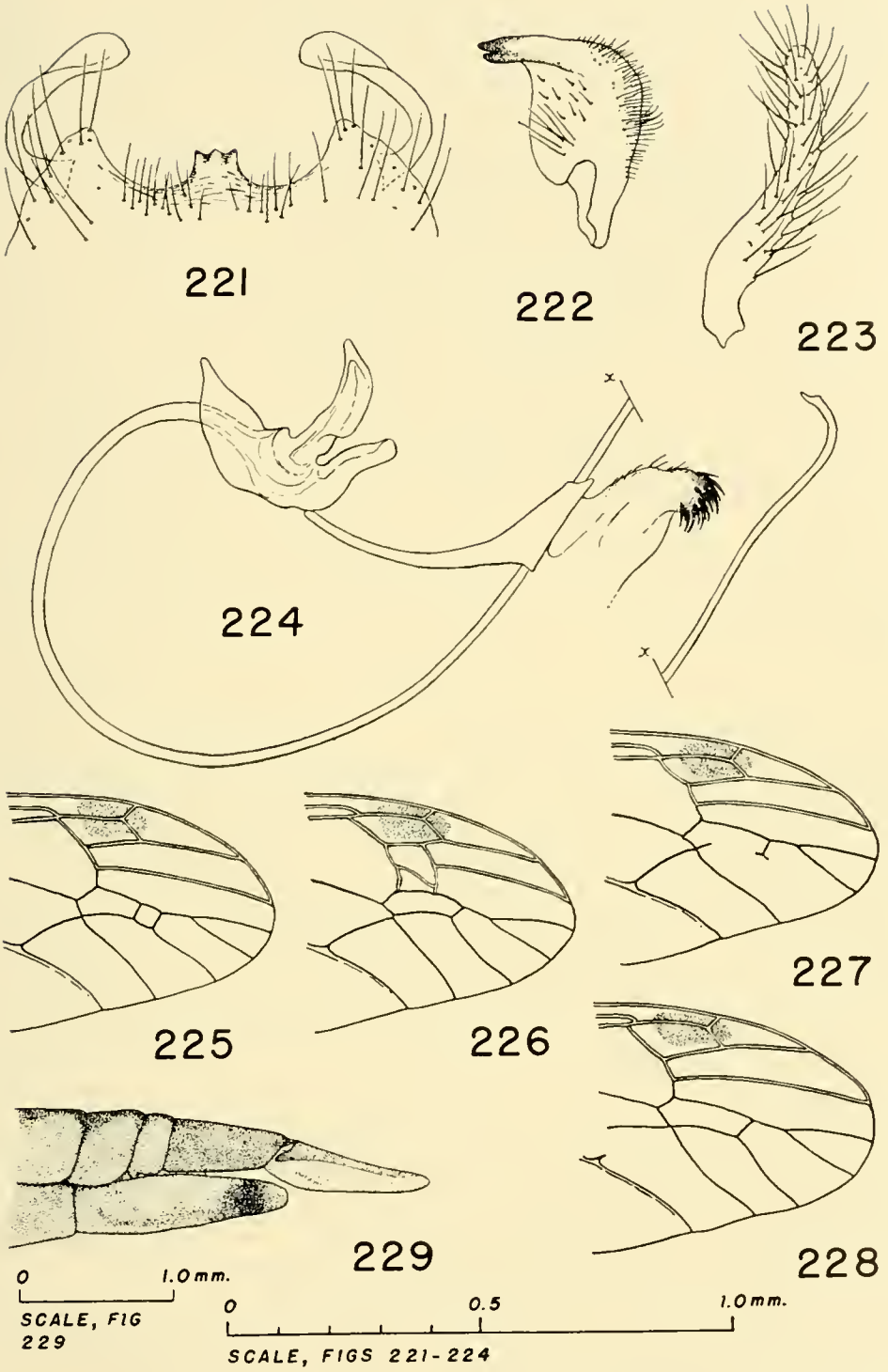
Diagnostic characteristics.—This species may be confused with *obscura, polita* sspp. and possibly with *johnsonella.* In the field, it may be distinguished from *polita* by its smaller size and distinct abdominal annulations; from *johnsonella* it differs in having the wings tinged with grayish brown instead of amber or golden brown. Field differentiation of *tridenticulata* from *obscura* should ordinarily not be attempted, for the reasons discussed under the latter species.

Male specimens of *tridenticulata* may be recognized readily by the configuration of the ninth tergum, with its characteristic three-toothed median lobe and slender tergal arms. In *polita cornuta* there is a tridentate median lobe, but the central tooth is invariably longer than the others and is often depressed; furthermore, the tergal arms and outer dististyles are conspicuously unlike those of *tridenticulata.* In female specimens of *tridenticulata,* the most darkly sclerotized part of the ovipositor is the subapical portion of the hypovalves, while in *obscura* females the tenth tergum is darkest. Females of all forms of *polita* have weaker abdominal annulations than *tridenticulata* or lack these altogether; in addition, the basal segments of the antennae of *polita* are paler than in *tridenticulata.*

Descriptive comments.—Dolichopeza tridenticulata, like *obscura,* is of a dusky brown color such that the flies are easily concealed in their shaded daytime haunts. However, where I have found the two species together, *tridenticulata* has usually been perceptibly lighter in over-all coloration. Particularly the thoracic dorsum is paler, being a dark reddish brown in *tridenticulata,* as described by Alexander, but dark brown in *obscura.* In the northern part of the range, *tridenticulata* is colored more nearly like *obscura.* In alcoholic collections of *tridenticulata* and *polita* sspp., flies often collected together in rocky ravine habitats, the former species may be recognized by the fact that the pleurotergite and a narrow portion of the other sclerites around the second spiracle are of the same shade of brown as the other sclerites of the thoracic pleura, while in *polita* these areas above the base of the haltere are darker than the rest of the pleura. This color difference is not evident in flies preserved dry.

Venational aberrations, especially those involving the media beyond its first fork, are widespread and very common in *tridenticulata.* Several of these were illustrated earlier (Figs. 40 through 48) in the discussion of intraspecific variation. These were regarded as locally inbred abnormalities. One specimen has been seen in which the m-cu cross-vein is broken and one segment of it strongly deflected (Fig. 228); in another, there is a spurious cross-vein in cell 1st M_2 (Fig. 225); and a third shows a most unusual abnormality of the branches of the radius (Fig. 226). Presence of the vein Sc_1 has been noted many times, and a few instances of failure of R_3 to reach the wing margin have been found.

Dolichopeza tridenticulata is one of the smaller species of *Oro-*



FIGS. 221-229. *Dolichopeza (Oropeza) tridenticulata;* 221—ninth tergum of male, 222—left inner dististyle of male, dorsal aspect, 223—left outer dististyle, dorsal aspect, 224—vesica, penis, adminiculum, adminicular rod and gonapophysis, left lateral aspect, 225-228—variations in wing venation, 229—terminal abdominal segments of female, left lateral aspect.

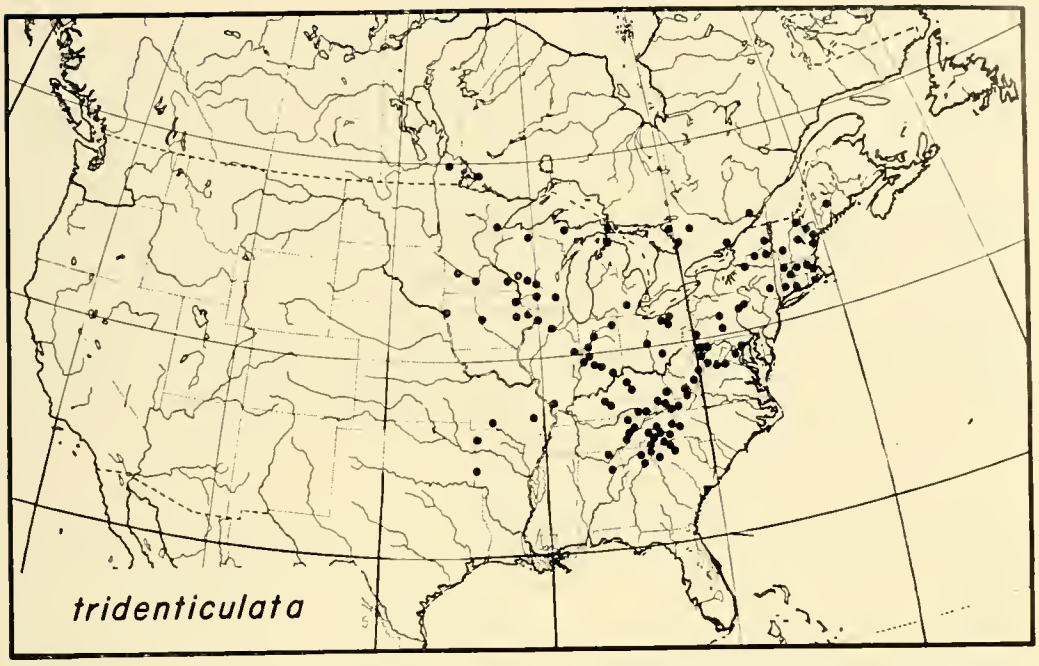
peza, nearly as small as *Dolichopeza (D.) americana.* Males average around 9 mm. in body length, with a 10.5 mm. wing, although they range from 7 to 10 mm. in length and have a variation in wing length from 8.8 to slightly over 12 mm. Females range in length of body from about 8 to 12.5 mm., their wings from 9 to 13 mm. The largest individuals of *tridenticulata* seen were from the Appalachian highlands of North Carolina and Virginia.

Variation in the profile of the medio-posterior margin of the ninth tergum of males consists primarily of the three widths of the subrectangular projection, as described earlier, under intraspecific variation. There are few localities in which *tridenticulata* has been taken where not all three of these forms are present. The commonest form, however, is that shown in Figure 221. The tergal arms are usually slightly flattened at their tips and may be somewhat widened (Fig. 221) or, less often, of uniform width throughout. The inner dististyle (Fig. 222) is very similar to that of *polita* sspp.

I have noticed that in many female specimens preserved either dry or in alcohol the cerci are deflected downward, so that the tips of the hypovalves are concealed. Why this happens in *tridenticulata* and not in *obscura, polita* or other species is not known. Antennae of females are about three-fifths as long as those of males taken at the same time and place.

Geographical distribution.—The geographical range of *tridenticulata* very closely approximates that of the three subspecies of *polita* combined. Collection records show that this species occurs from Maine westward to southeastern Manitoba, southwestward to the Ouachita Mountains, and southward along the Appalachian Mountains to northeastern Georgia. It must be much more widespread in southeastern Canada than present records indicate, and collections in western Arkansas, southern Missouri, and Iowa only sketchily outline its distribution along the edge of the plains. *Dolichopeza tridenticulata* will probably eventually be found in eastern Oklahoma and Kansas, possibly in Nebraska and eastern North and South Dakota. It may also occur in the Turtle Mountains of North Dakota and in the Black Hills of South Dakota. I would not expect it to range very far northwest across Canada beyond the presently known range.

Habitats.—In my experience, *tridenticulata* is primarily a rock gorge species; at least, it is in such habitats that I have found this species in the greatest numbers. Although I found it locally



MAP 10. Range of *Dolichopeza (Oropeza) tridenticulata* Alexander. Each spot represents one or more collections within a county (United States) or at a locality.

abundant in certain northern woodlands, it was never as common there as in many rocky Appalachian ravines and rock ledge gorges in Indiana and Ohio. The only published habitat data are from the mountainous region of western North Carolina, where Alexander (1941a: 297) found *tridenticulata* ". . . common under low earthen banks along road." In the vicinity of rocky ravines and boulder-strewn, forested mountainsides, *tridenticulata* is often taken away from the actual rocks, in such places as culverts, outhouses and other man-made shelters, open drain tiles, and beneath exposed tree roots, overhanging banks, or almost any other situation affording deep shade. They were frequent visitors in my tent, in Indiana, even when I had pitched it several hundred yards back from the rocky ravine where the flies were usually found by day. They always arrived during the night, in such cases, and frequently stayed until darkness fell again.

In the northern forests, *tridenticulata* was most often taken in or about small buildings, such as outhouses and picnic shelters. In some localities, it was found among granite boulders, where these were so arranged on a slope as to provide small, darkened crannies, here and there. In other localities, however, there were no rock outcrops seen, and the relief was so low that there could not have been any ravines; in one such place, *tridenticulata* was reared from a scanty growth of moss on a tree trunk.

Locally and in season, *tridenticulata* forms great swarms in shaded niches in the rocks, often in the company of *polita* and other species. At such times, one may easily capture hundreds of specimens. Because of this dense swarming, it seems to me a little unusual that prior to the beginning of this study only about 200 specimens of *tridenticulata* had been collected in all of North America, as far as I am able to tell. During periods of heaviest emergence in the gorges of southern Indiana, for example, it is possible to collect 200 individuals easily within ten minutes, and I have often stopped collecting only because I was satisfied that further examples of the species would not alter the characteristics of my sample.

Seasonal distribution.—Although there are collection records for all the summer months for practically all parts of the range, there is also good evidence of two annual peaks of emergence, in most localities. From Georgia and Arkansas northward to New England and southern Michigan and Minnesota, these peaks fall in June and August, locally about a week after the appearance of *polita.* In Parke County, Indiana, in 1953, the first individuals of *tridenticulata* were collected on 1 June, which was about two weeks after *americana* began to emerge, nine days after *polita cornuta,* four days after *walleyi* and *obscura,* and the same day as *carolus* first appeared. Peak numbers are reached about mid-June, in Indiana, and again between mid-August and early September. By 10 July, a few females were still present in the Parke County locality just mentioned. In another year, 28 August seemed almost the end of the late summer emergence of *tridenticulata* in nearby Owen County, Indiana. As in several other species, there appears to be a rather prolonged, single mid-summer period of emergence of adults of *tridenticulata* in northernmost United States and southern Canada. In northern Michigan, I found the peak of abundance to be about mid-July.

Individuals of the late summer generation are not conspicuously smaller than those taken in June.

Immature stages.—Average measurements of eggs from several females of *tridenticulata* are .65 by .30 mm. There is a well-developed terminal filament. Early instar larvae are unknown, but the third and fourth instars have been found in various relatively dry mosses. Larvae and many pupal skins were recovered from the moss *Dicranella heteromalla,* growing on the rather dry, upper surfaces of blocks of rock in wooded, rocky habitats in Ohio and Missouri. Pupae were obtained from *Tetraphis pellucida* where that

moss was growing together with a powdery lichen, on a shaded sandstone cliff. The only specimens of *tridenticulata* known from southern Michigan are those reared from larvae collected from sparse tufts of the moss *Orthotrichum sordidum* that were growing in crevices of the bark of a tree, five feet above the ground. Larvae taken in the dry moss, *Hedwigia albicans*, and described as those of *obscura* (Alexander, 1920: 983) were found to be *tridenticulata*. The larva is very similar to that of the closely related *polita*, but is smaller and has the pleural hairs of the eighth abdominal segment irregularly arranged, leaving bare areas. These two species stand apart from all others in the genus, in that their larvae have the pleural hairs thickened and not arranged in circular groups.

Pupae of *tridenticulata* may be identified by the spiracular yoke, which is similar to that of *polita*. The yoke is broadly but shallowly emarginate, the emargination lacking the inner, rounded "shoulders" seen in *polita* and thus appearing very broadly V-shaped. In a sample of 16 pupae from Carter County, Missouri, all but three had a spiracular yoke as shown in Figure 122, the three having a shallower emargination. In this same group of pupae, 11 had no spinous processes on the fourth abdominal sternum and 5 had these developed to some degree. It was noted that in a few specimens the middle pair of spinous processes of the eighth sternum were barely close enough together to be regarded as of the usual form for the *obscura* group; such specimens, however, cause no difficulty in use of the key to pupae. The pupal stadium, under laboratory conditions, was six days.

Notes on distribution.—Alabama—Etowah County, 26 June; Madison County, 8 June. Arkansas—Polk County, 30 July; Washington County, 30 July. Connecticut—Litchfield County, 9 July; New Haven County, 4 to 18 July. Georgia—Lumpkin County, 7 June; Stephens County, June; Towns County, 12 June; Union County, 23 May, 9-10 and 28 June. Illinois—Carroll County, 7 July; Jackson County, 4 June; La Salle County, 7 July; Vermilion County, 13 June. Indiana—Allen County, 10 July; Cass County, 8 June; Jefferson County, 2 to 23 June and 20 August; Montgomery County, 28 June; Monroe County, 23 June; Owen County, 4 to 7 and 18 to 27 June and 28 August; Parke County, 1 and 9 to 28 June, 10 July, and 11 to 30 August; Tippecanoe County, 20 June. Iowa—Boone County, 21 to 29 June; Clayton County, 8 July; Jackson County, 8 July; Linn County, 8 July; Woodbury County, 11 June. Kentucky—Barren County, 2 August; Bell County, 18 June; Edmonson

County, June (?); Franklin County, 23 June; Garrard County, 23 June; Letcher County, 3 July; Pike County, 3 July; Whitley County, 24 June. MAINE—Cumberland County, 13 August; Oxford County, 11 July; Penobscot County, 25 June to 5 July; York County, 1 July. MANITOBA—West Hawk Lake (near Rennie), 3-4 August. MARYLAND—Garrett County, 26 June; Montgomery County, 24 May to 28 June. MASSACHUSETTS—Berkshire County, 19 June; Franklin County, no date; Hampshire County, 1 July; Middlesex County, 11 July; Norfolk Co., 18 June. MICHIGAN—Cheboygan County, 5 to 30 July; Chippewa County, 13 July; Marquette County, 13 to 15 July; Washtenaw County, 14 May. MINNESOTA—Blue Earth County, 8 July; Carlton County, 6 August; Redwood County, 8 July; Winona County, 7 July. MISSOURI—Carter County, 6 June; Taney County, 10 to 20 June. NEW HAMPSHIRE—Coos County, 11 July; Grafton County, 14 July. NEW YORK—Essex Co., 1 July; Hamilton County, 12 July; Oneida County, 20 June and July; Ulster County, 28 June; Warren County, 2 July. NORTH CAROLINA—Buncombe County, 30 May; Burke County, 14 and 21 June, 1 July; Haywood County, 28 July; Macon County, 11 to 20 June; Swain County, 30 June; Transylvania County, 9 to 14 June; Yancey County, 26 May to 20 June, and 7 July. OHIO—Delaware County, May and 6 to 14 June; Geauga County, 17 July; Hocking County, 30 May and 6-7 June; Medina County, 4 July; Portage County, 24-25 June, 14 July, and 16 August. ONTARIO—Algonquin Park, 23 June and 10 August; Gananoque, 8 July; Go-Home Bay (Georgian Bay), 22 June; Kenora District (Lake of the Woods), 4 August; Pte. au Baril (Georgian Bay), 6 to 16 July and 15 August. PENNSYLVANIA—Centre County, 25-26 June and 9 July; Columbia County, 15 July; Huntington County, 9 July; Luzerne County, 27 June and 5 to 10 July; Westmoreland County, no date. QUEBEC—Rigaud, 25 June. SOUTH CAROLINA—Greenville County, 7 June and 1 September; Pickens County, 29 June. TENNESSEE—Bledsoe County, 26 June; Blount County, 20 May; Cumberland County, 25 June; Fentress County, 31 May to 20 July; Morgan County, 12 June; Sevier County, 7 to 23 June. VERMONT—Windsor County, 7 July. VIRGINIA—Fairfax County, 30 June and 5 September; Giles County, 1 June to 7 July and 20 July to 1 August; Rockingham County, 6 July; Shenandoah National Park, 28-29 June and 6 July; Smyth County, 20 June; Washington County, 20 June and 2 July; Wise County, 2 July. WEST VIRGINIA—Greenbrier County, 4 July; Pendleton County, 26-27 June;

Pocahontas County, 23 June and 5 July; Preston County, 25 June and 5 August; Randolph County, 5 July; Tucker County, 24-25 June and 6 August. WISCONSIN—Iron County, 6 August; Jefferson County, 21 June and 21 July; Juneau County, 6 July; Monroe County, 6 July; Sauk County, 5 July; Trempealeau County, June and 7 July.

Dolichopeza (*Oropeza*) *venosa* (Johnson)

Literature references.—*Oropeza venosa* Johnson. Johnson, 1909: 120, pl. 15 (hypopygium); Alexander, 1919: 930; Alexander, 1922b: 61; Alexander, 1924: 59-60; Alexander, 1925: 172; Johnson, 1925: 33; Alexander, 1928: 57; Leonard, 1928: 698; Alexander, 1929a: 236; Alexander, 1929b: 25; Alexander, 1930a: 212; Alexander, 1931a: 139.

Dolichopeza (*Oropeza*) *venosa* (Johnson). Alexander, 1936: 280; Alexander, 1942: 215, fig. 26J (hypopygium).

Original description.—"Front and rostrum yellow, vertex and occiput dark brown, palpi brown, antennae yellow, becoming fuscous beyond the first joint of the flagellum. Thorax yellowish with three broad, dark brown stripes, the dorsal stripe ending at the suture, the lateral stripes abbreviated anteriorly and interrupted at the suture; plurae subtranslucent; collar, scutellum, metanotum, a large spot on the center of the plurae, smaller spots at the base of the halteres and between the coxae dark brown. The black bands of the abdomen are united along the dorsal line, leaving a large yellow spot on the side of each segment. Halteres long, yellow; knobs dark brown. Legs light yellow, the tarsi yellowish white. Wings brownish hyaline; stigma and veins dark brown, the radial and cubital veins noticeably prominent, and the short median cubital cross-vein wanting. Genitalia brown, appendages black, style long, reaching the end of the penultimate segment, reddish, base black; appendages at the base of style acute, brown, tipped with black, margin deeply emarginate. Length, 10 mm."

Types.—Holotype male, Mt. Greylock (Berkshire County), Massachusetts, 15 June 1906, C. W. Johnson. Five paratypes, all males, from Brookline, Massachusetts, Moosehead Lake, Maine, Bartlett and Hanover, New Hampshire, and St. Johnsbury, Vermont. These six specimens are in the collection of the Museum of Comparative Zoology, Harvard University. Another male in this collection, from the type locality, 11 June 1906, but without a paratype label, is probably a paratype and the seventh specimen mentioned by Johnson (1909: 120).

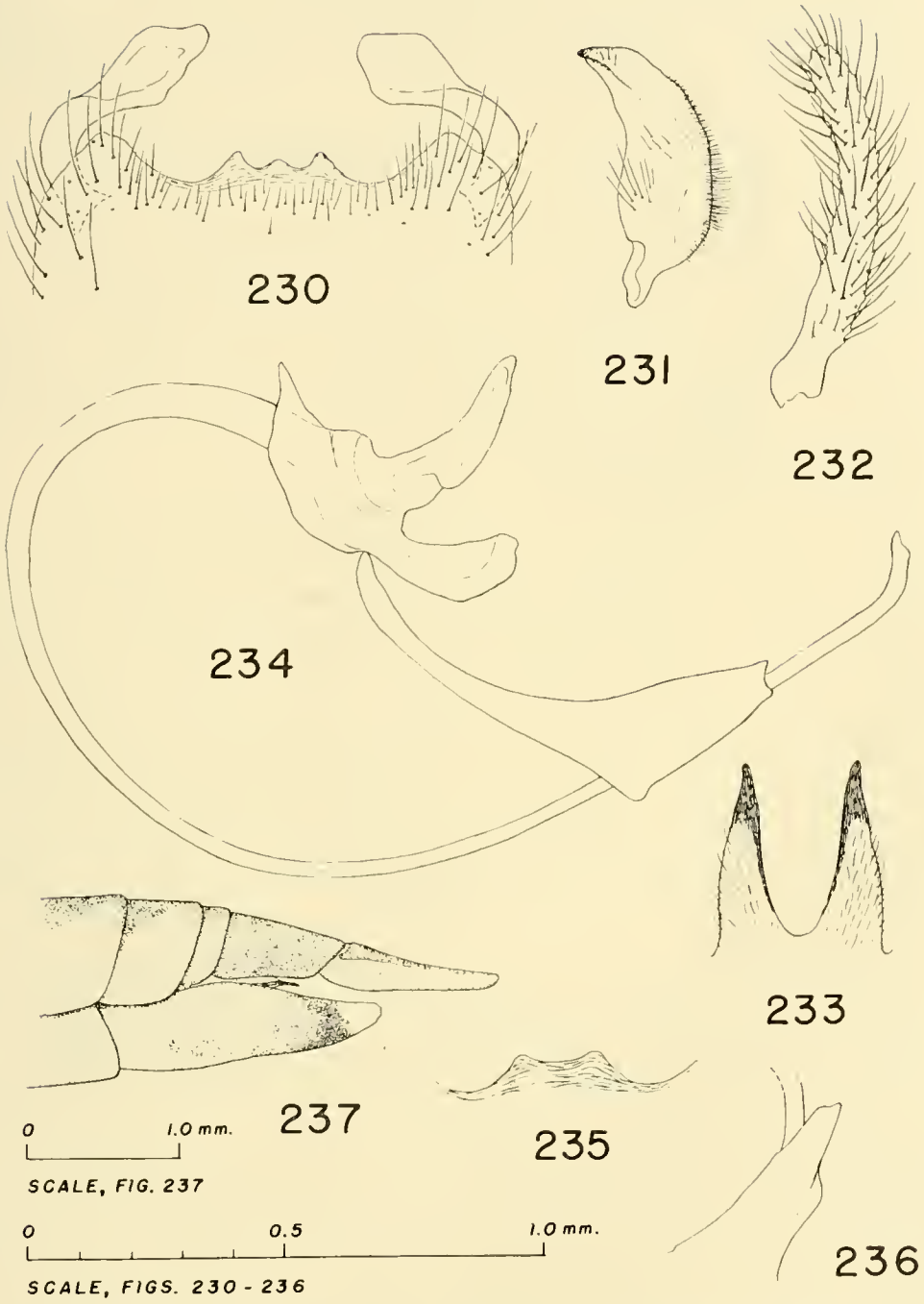
Diagnostic characteristics.—Dolichopeza venosa rather closely resembles both *carolus* and *subalbipes,* not only in general coloration but also in resting posture, but it differs from both in having yellowish instead of white tarsi and in lacking darkened tips on the femora and tibiae. Darker than *carolus* in over-all aspect, although like that species colored generally dark brown on tawny or dark buff, *venosa* is less contrastingly colored than subalbipes, which is more of a brownish black on yellowish buff. This coloration is particularly evident in the abdominal region. The prescutal stripes of *venosa* are more distinct than those of either *carolus* or *subalbipes.* This species is somewhat darker than the closely related *subvenosa,* a difference useful only in comparison of the two species.

Having long, acutely tipped, blackened gonapophyses (Fig. 233), males of *venosa* may be quickly separated from all other species except *subvenosa.* From that species, they may be distinguished by characteristics of the tergal arms and the adminiculum. The margin of the spatulate tip of the tergal arm in *venosa* is ordinarly angular (Fig. 230), but it is rather evenly curved in *subvenosa;* and *venosa* lacks the well-developed ventral spine found on the adminiculum of *subvenosa.* The inner dististyles of *venosa* (Fig. 231) are usually slender subapically but broadened in *subvenosa.*

Females of *venosa* may be recognized by the combination of the color characteristics described above with the intense subapical sclerotization of the hypovalves. They are separable from females of *subvenosa* on the basis of geographical range and, less reliably, by their darker color.

Descriptive comments.—Color variation in this species is particularly noticeable in the intensity of over-all coloration, certain individuals (usually males) appearing nearly as dark as *johnsonella* or even *obscura,* when seen from a distance of several inches. Coloration of the legs, especially of the femora, may be brown to yellowish brown, and the tarsi may vary from a very pale tan through yellowish white to almost white. The extent of the stigmal spot of the wing varies, being somewhat smaller in specimens from Wisconsin and Minnesota than elsewhere.

Venation in *Dolichopeza venosa* is very stable, as compared to some species in the *obscura* group. I have seen only three instances of an open cell 1st M_2 (discal cell) by loss of the medial cross-vein. One of these is a paratype, in which the abnormality was noted by Johnson. Half a dozen specimens seen had the veins M_{1+2} and M_3



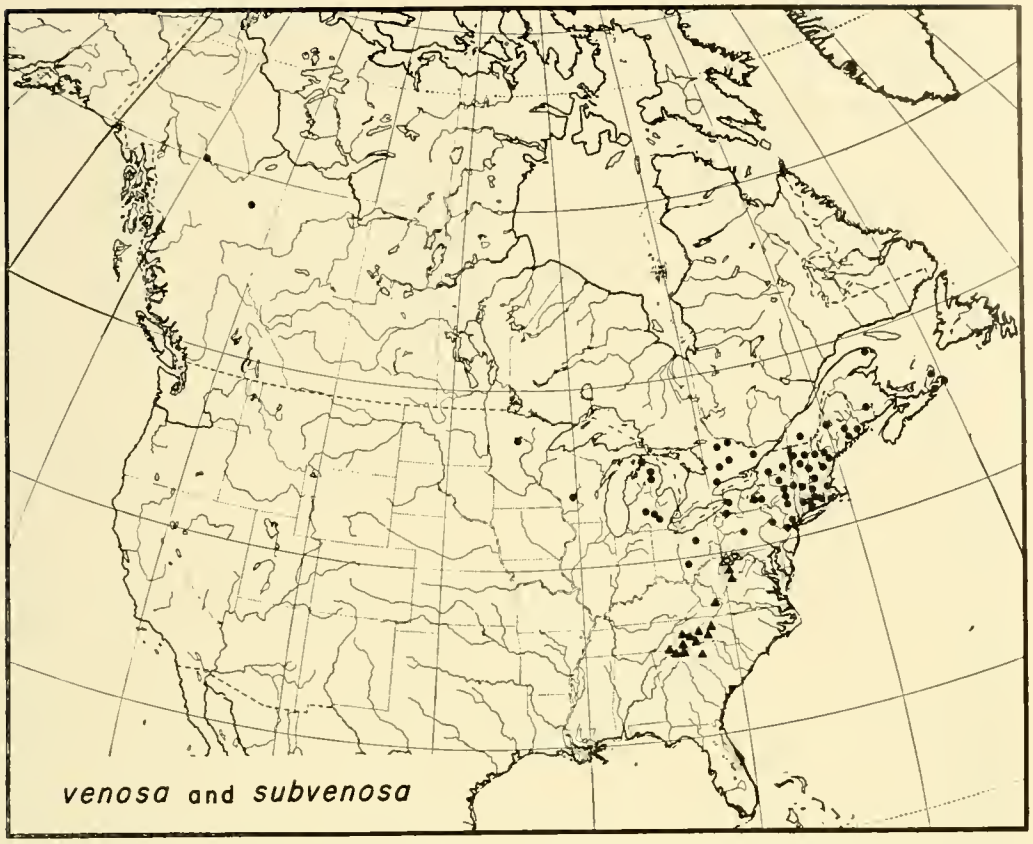
FIGS. 230-237. *Dolichopeza (Oropeza) venosa;* 230—ninth tergum of male, 231—left inner dististyle of male, dorsal aspect, 232—left outer dististyle, dorsal aspect, 233—gonapophyses, ventral aspect, 234—vesica, penis, adminiculum and adminicular rod, left lateral aspect, 235—variation in medio-posterior margin of ninth tergum of male, 236—adminiculum of male holotype, left lateral aspect, 237—terminal abdominal segments of female, left lateral aspect.

both joined with M_4 at the m-cu cross-vein; that is, the short length of M_{3+4} was missing. It is not unusual for the vein Sc_2 to join R_1 well beyond the origin of the radial sector. Johnson described the m-cu cross-vein as lacking; he referred to a short length of M_4 that results from the intersection of m-cu with M_4 instead of the junction of M_3 and M_4, but actually this disposition of the veins is not at all uncommon. A long, sloping medial cross-vein has been seen in two specimens, and a distally spurred cross-vein in only one.

Body length of males varies from 10 to 11.5 mm.; wings from 11.5 to 13 mm. Females measure 10 to 13 mm., their wings also from 10 to 13 mm. The smaller specimens are from Wisconsin and Minnesota, and the larger ones are from the central and northern Lower Peninsula of Michigan.

There is a great amount of variation in the profile of the ninth tergum of the males, although the medio-posterior projection ordinarily consists of a broad, three-lobed or three-pointed prominence. As in *subalbipes*, the central point or lobe is sometimes lost (Fig. 235). In a collection of 38 males of *venosa* from Eaton County, Michigan, I found 14 shapes of this part of the ninth tergum. Eighteen specimens resembled the form shown in Figure 230, two had two small median points, four lacked the central point but varied in the depth of the emargination, one had an accessory lateral lobe, and the other types were variations of the relative lengths of the central and lateral lobes. In this same group of 38 males, 27 had irregularly angular apical portions of the tergal arms, three had these rounded as in *subvenosa*, and eight were classed as intermediates. Rounded margins of the apical part of the tergal arm have also been seen in specimens from other parts of the range. Among the 38 males mentioned, 27 had inner dististyles somewhat suggestive of those of *subvenosa*, 11 as illustrated in Figure 231; 26 had no vestige of a spine on the adminiculum, but one had a spine about half as long as that found in the typical form of *subvenosa*, while 11 were of intermediate form. In specimens from New York, Connecticut and Massachusetts, I have seen various developments approaching the adminicular spine; in fact, the holotype of *venosa* has a low, rounded protuberance in the same position as that occupied by the spine in *subvenosa* (Fig. 236).

Geographical distribution.—Dolichopeza venosa occurs from Nova Scotia and the Gaspé Peninsula westward to Minnesota, northwestward to British Columbia and the Yukon, and southward



MAP 11. Range of *Dolichopeza (Oropeza) venosa* (Johnson) and *Dolichopeza (Oropeza) subvenosa* Alexander. Solid circles—*venosa;* solid triangles—*subvenosa;* circle within triangle—area where both forms occur. Each spot represents one or more collections within a county (United States) or at a locality.

to Ohio and Maryland. I have not seen the specimens from western Canada, which were collected by Dr. Alexander on his Alaskan trip in the summer of 1952, but I had rather expected that *venosa* ranged well northwest of Minnesota and northern Michigan, on the basis of the ecological distribution of the flies. The wide gap between the ranges of *venosa* and *subvenosa* that obscured their spatial relationships for many years was closed in the summer of 1958 with the discovery of both forms in northern West Virginia. My reasons for not regarding these two forms as subspecies have already been presented in the discussion of *subvenosa.*

Habitats.—This species has been found associated with the rocky ravine type of environment in some localities and elsewhere with cool, moist northern forests. Often, these habitats are combined. Deeply shaded crannies in a northern hardwood forest in Cheboygan County, Michigan, occupied mostly by *obscura,* were shared by *venosa;* and in Juneau County, Wisconsin, *venosa* was taken together with *polita,* under sandstone ledges. The *venosa-polita* asso-

ciation in a rocky habitat was found again in Eaton County, Michigan, where large numbers of both species were taken on the same date. In Centre County, Pennsylvania, *venosa* was swept from deep grasses at the edge of a hemlock-hardwood forest, where the forest opened rather abruptly into a mountaintop marsh. The habitat at Lake Itasca, Clearwater County, Minnesota, was in many ways similar to this. In general, forested areas, especially where these are also rocky, appear to be the most suitable environment for *venosa*, and much of the northeastern part of the United States and southeastern Canada comprises such an environment. Within this widespread habitat, *venosa* seems to be nowhere very abundant. Only once, in Eaton County, Michigan, have I seen aggregations of this species.

Seasonal distribution.—There are a few records for May, and most of the specimens are males, females appearing in the last days of that month. Most of the July records, on the other hand, are for females and are sporadic after the first week of the month. Records of June collections are by far the most numerous and point to a single early summer period of emergence, the peak coming in the last two weeks of June in most vicinities shown on the map, but several days earlier in the southern Ohio (Hocking County) locality.

Immature stages.—Eggs of this species, taken from a female of average size, measured about .79 by .32 mm. They have no terminal filament. Eggs laid on the nights of 31 May through 2 June began to hatch on 8 June, indicating the egg stadium to be about seven days. Four females, caged in the laboratory, produced over 300 eggs, each fly retaining several; accordingly, a female probably matures around 100 eggs. The larvae bear a striking resemblance to those of *subalbipes*, in that both species have the larger microscopic hairs of the dorsum arranged in irregular, interrupted and staggered or deflected transverse rows, which are short with the hairs long and densely set. This arrangement makes it virtually impossible to count the number of transverse ridges on any segment. Larvae were found in rather dry cushions of the moss *Plagiothecium roeseanum* that was growing on small amounts of soil trapped on a shaded sandstone cliff. It seems certain that this moss microhabitat was periodically well wetted by surface runoff and retained this moisture for many days. Nearby, on moist sand at the base of a cliff over which seepage water flowed, the moss *Leptobryum pyriforme* was growing, and there also larvae of *venosa*

were found. The pupa is characterized by having conspicuous spinous processes on the posterior ring of the fourth abdominal sternum and by the spiracular yoke, the lobes of which are about twice as long as their basal width. It has been noted that the burrows prepared by the last instar larvae for pupation are unusually long, being about one and three-fourths to twice as long as the pupa. The duration of the pupal stadium is ordinarily six days; one female emerged on the eighth day but was abnormal and died before becoming completely freed of the pupal skin.

Notes on distribution.—BRITISH COLUMBIA—47 miles south of Fort Nelson, Alaska Highway milepost 253, 25 June. CONNECTICUT—Hartford County, 8 to 10 June; Litchfield County, 9 to 13 June; New Haven County, 29 June; Tolland County, 14 June; Windham County, 14 June. MAINE—Cumberland County, 1 July; Hancock County, 15 to 22 June; Oxford County, 11 July; Penobscot County, 25 June to 5 July; Piscataquis County, 11 July; Washington County, 15 July. MARYLAND—Garrett County, 28 June (*subvenosa* also here). MASSACHUSETTS—Berkshire County, 15 to 28 June; Hampshire County, 15 June; Norfolk County, 30 May and 18 June. MICHIGAN—Cheyboygan County, 22 to 30 June; Eaton County, 28 to 31 May; Livingston County, 11 June; Ogemaw County, 20 June; Oscoda County, 16 to 26 June; Washtenaw County, 4 June. MINNESOTA—Clearwater County, 16 June. NEW BRUNSWICK—Fredericton, 20 June. NEW HAMPSHIRE—Carroll County, 2 July; Cheshire County, 18 June; Coos County, 2 to 22 July; Grafton County, 5 July. NEW JERSEY—Bergen County, 1 to 15 June; Essex County, June; Morris County, July. NEW YORK—Albany County, 18 June; Cattaraugus County, 30 June; Cortland County, 21 July; Erie County, 4 to 23 June; Essex County, 16 June; Fulton County, 15 to 25 June; Greene County, June; Hamilton County, 17 to 23 June; Herkimer County, 9 June; Rensselaer County, mid-June; Tompkins County, 5 June. NOVA SCOTIA—Cape Breton County, 4 July; Richmond County, 1 July; Victoria County, 2 July. OHIO—Hocking County, 20 May; Portage County, 24 June. ONTARIO—Algonquin Park, 3 to 29 June; Burke Falls, 9 to 13 July; Gull Lake (Muskoka District), June; Orillia, 26 June to 2 July; Sand Lake (7 miles north of Gananoque, called "Sand Bay" on some maps), 2 July; Toronto, 17 June. PENNSYLVANIA—Centre County, 25 June; Luzerne County, 2 to 7 and 29 June. QUEBEC—Knowlton, 26 June; north shore Gaspé Peninsula, July. VERMONT—Caledonia County, 27 June; Chittenden County, 15 to 24 June; Washington County, 17 June. WEST VIR-

GINIA—Preston County, 25 June (*subvenosa* also here). WISCONSIN —Juneau County, 6 July. YUKON—Watson Lake, Alaska Highway milepost 632, 28-29 June.

Dolichopeza (*Oropeza*) *walleyi* (Alexander)

Literature references.—Oropeza walleyi Alexander. Alexander, 1931a: 139-140.

Dolichopeza (*Oropeza*) *walleyi* (Alexander). Alexander, 1936: 280; Alexander, 1940: 618; Alexander, 1941a: 297; Alexander, 1942: 216, fig. 26K (hypopygium); Rogers, 1942: 60; Rogers, 1949: 12; Whittaker, 1952: 34; Foote, 1956: 222.

As *Oropeza sayi* Johnson. Johnson, 1909: 118-119 (part); Alexander and McAtee, 1920: 393 (at least part); Rogers, 1930: 23; Rogers, 1933: 35, 49.

As *Oropeza similis* Johnson. Dickinson, 1932: 212, fig. 113 (wing).

As *Dolichopeza* (*Oropeza*) *dakota* Alexander. Alexander, 1944: 241-243 (new synonymy).

Original description.—"General coloration brownish yellow, the praescutum and scutum with clearly-defined brown areas; head gray; pleura yellowish white, without distinct markings; halteres with slightly infuscated knobs; legs pale brownish yellow; wings brownish yellow, the stigma brown; abdominal tergites obscure yellow with a brown median stripe, the lateral margins not darkened; male hypopygium with the gonapophyses large and conspicuous, the margins irregularly dentate. Male. Length, about 9-10 mm.; wing, 11-11.5 mm. Female. Length, 11-12 mm.; wing, 12 mm.

"Frontal prolongation of head pale yellow; palpi pale, the terminal segment suddenly blackened. Antennae (male) elongate, the basal three segments (male) or two segments (female) yellow, the remaining segments passing into brown, the basal enlargements a trifle darker. Head gray, with a dark median and posterior border, the occiput paler.

"Mesonotal praescutum brownish yellow, with three very distinct and clearly defined brown stripes; scutum similar, each lobe with two confluent dark brown areas; scutellum and postnotum pale brownish testaceous. Pleura yellowish white, without distinct dark markings, only the sternopleurite a little darkened. Halteres yellow at base, darkened outwardly, the knobs slightly infuscated. Legs with the coxae and trochanters yellow; remainder of legs

pale brownish yellow. Wings brownish yellow, the costal region deeper yellow; stigma oval, conspicuous, brown; obliterative areas before the stigma and across the base of cell 1st M_2; veins brown.

"Abdominal tergites obscure yellow, with a dorso-median brown stripe, the lateral margins pale; sternites yellow, with a dark spot at the incisures, the outer segments more uniformly darkened. Male hypopygium with the caudal margin of the tergite with a broad V-shaped notch that is extended into a flattened flange bearing a small slender spine at base of notch; lateral arms of tergite expanded at tips into obtuse blades. Outer dististyle long and slender, the base not enlarged. Inner dististyle dilated, produced into a blackened beak that is unequally bidentate. Gonapophyses very large and conspicuous, yellow, the margins irregularly dentate."

Types.—Holotype male, Knowlton (Brome County), Quebec, 4 July 1929, G. S. Walley. Allotype, same locality and collector as holotype, 12 July 1929. Alexander (1931a: 140) listed in addition to the holotype and allotype "paratopotypes, 3 males and females, June 29-July 12, 1929 (G. S. Walley); paratypes, 2 males, Brookview, Rensselaer County, New York, June 14-21, 1923 (C. P. Alexander)." The holotype and one paratype of each sex are in the Canadian National Collection, in the care of the Department of Agriculture, Ottawa, Ontario. The allotype, one male paratopotype and a female specimen from Brookview, New York, 14 June 1923, labelled paratype, are in the collection of Dr. Alexander, in Amherst, Massachusetts. The present location of the other specimen or specimens from the type series is unknown to me.

Diagnostic characteristics.—Field recognition of *walleyi* is usually possible on the basis of a combination of appearance of the fly and the type of environment. When it rests by day in deeply shaded crannies beneath rock outcrops, together with species of the *obscura* group, *walleyi* may be easily recognized by its conspicuously paler thoracic pleura. From *carolus, subalbipes, venosa* and *subvenosa,* species with which it often occurs in leafy, low vegetation, *walleyi* is distinguished by its darker tarsi, which are never as pale as the darkest in those species. Occasionally, I have taken *walleyi* together with its nearer relatives, *sayi* and *dorsalis,* in swamp margins, and *similis,* in swampy woods. In such cases, sight recognition is difficult and not reliable; specimens should be captured before identification is attempted.

Males of *walleyi* may be readily identified by their gonapophyses, which are yellowish in color, flattened and flared at their tips and

have irregularly toothed margins. Although in caudal, or ventral, aspect the gonapophyses of *walleyi* are very like those of *similis,* they do not have the heavy spine projecting from the inner face of each gonapophysis, as in *similis.* The gonapophyses in *sayi,* the only other species in which these structures resemble those of *walleyi,* are only slightly widened at their tips and have the margins entire.

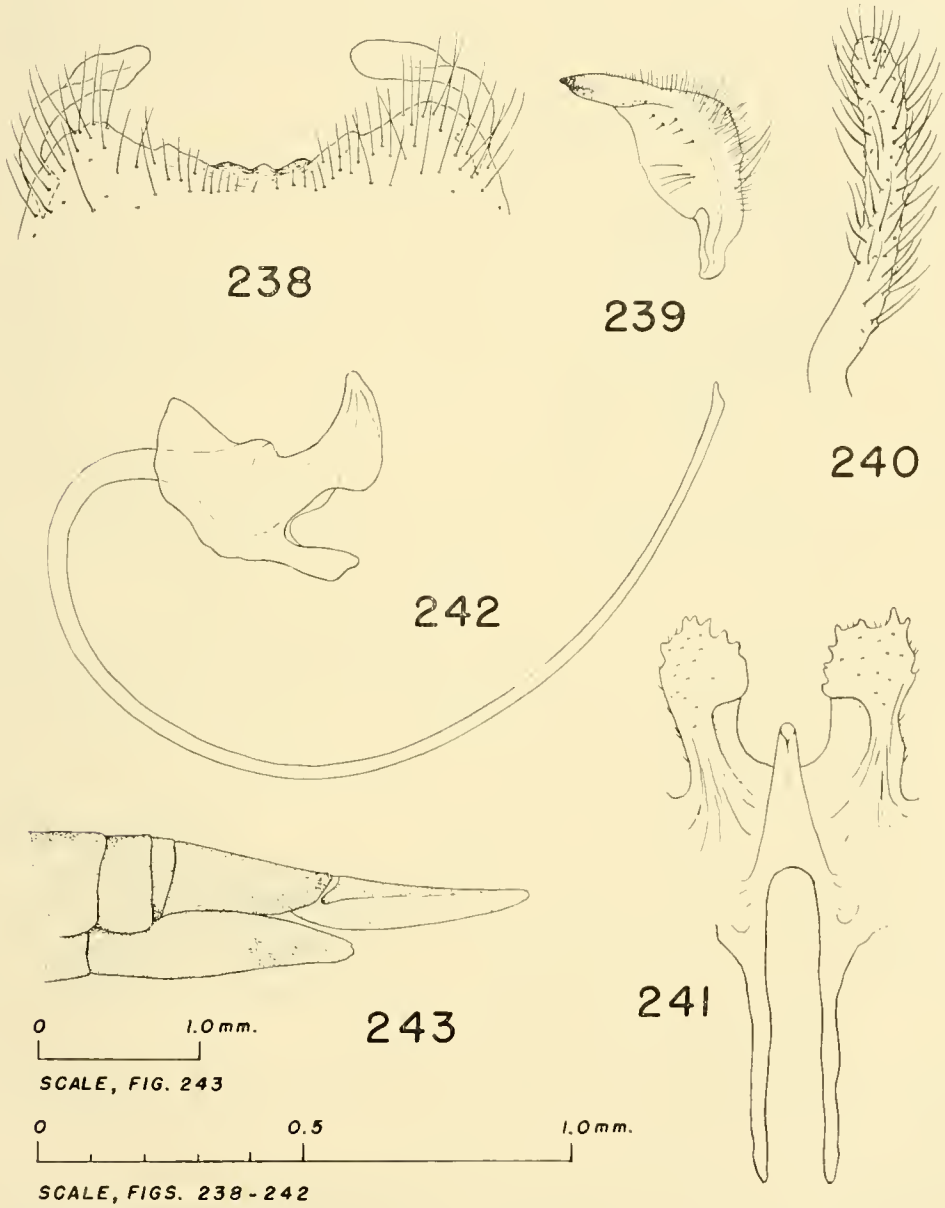
Both males and females of *walleyi* may be recognized by their coloration, the yellowish body, yellowish brown legs and darkened thoracic dorsum together resembling, in a general way, only *sayi, dorsalis* and *similis.* The prescutal stripes in *walleyi* are, through most of the species' range, reddish brown, as compared with the nearly black stripes of *sayi* and the more brown but nearly obliterated stripes of *similis* and *dorsalis.* Where *walleyi* overlaps the range of *sayi,* the thoracic pleura are unmarked, or nearly so. There may be a slight darkening of the ventral part of the pre-episternum and mesothoracic meron, but this is never intense enough to be confused with the dark gray pleural markings of *sayi.* Outside the range of *sayi,* both sexes of *walleyi* take on color characteristics similar to those of *sayi,* so that females are most reliably identified by association with males.

Descriptive comments.—As pointed out earlier, in the discussion of intraspecific variation, the transition from unmarked to strongly marked thoracic pleura and the correlated transition from reddish brown to grayish brown thoracic stripes in *Dolichopeza walleyi* is not abrupt. Moving southward and westward from the center of the range of *sayi,* one first encounters noticeably marked or darkened populations of *walleyi* in Georgia, Tennessee, Indiana, Illinois, southern Minnesota and Saskatchewan. Specimens of *walleyi* collected south and west of the line indicated are increasingly strongly pigmented as their locality is farther from the line, so that the outermost populations, such as those from Florida, southern Missouri, eastern Kansas, western Iowa and the Black Hills of South Dakota, greatly resemble *sayi* in most details of coloration.

The single female specimen on which *Dolichopeza* (*Oropeza*) *dakota* is based (Alexander, 1944:241-243) has distinct grayish brown thoracic stripes and dark pleural markings; it has a seam of dark color along the cubitus and a rather darkly colored stigmal spot; and the subapical sclerotization of the hypovalves is quite dark. In all, this fly much more nearly resembles eastern *sayi* than

it does the paler eastern form of *walleyi*. It was probably the intensity of the coloration that led Alexander to regard *dakota* as nearest to *venosa*. Having collected a large number of both sexes of the dark form of *walleyi* in the Black Hills and having compared females from among these with the holotype of *dakota*, I am convinced that *dakota* should be placed in the synonymy of *walleyi*.

Venational variation in *walleyi* includes the branching of M_3 together with M_{1+2} from the first fork of the media, so that M_3



FIGS. 238-243. *Dolichopeza (Oropeza) walleyi;* 238—ninth tergum of male, 239—left inner dististyle of male, dorsal aspect, 240—left outer dististyle, dorsal aspect, 241—gonapophyses, adminiculum and adminicular rods, dorsal aspect, 242—vesica and penis, 243—terminal abdominal segments of female, left lateral aspect.

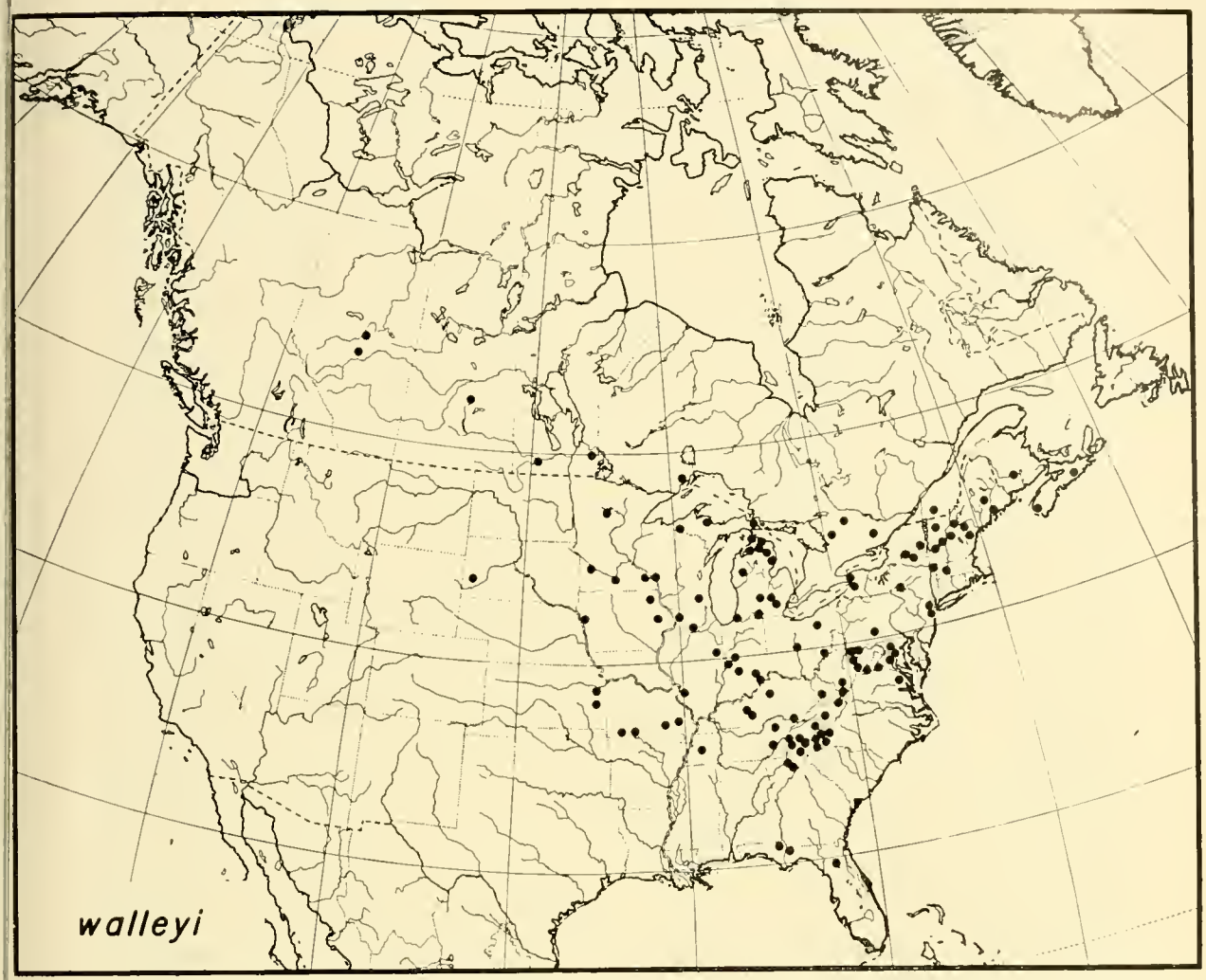
has no connection with M_4, a fragment of a spurious cross-vein in cell M_2, a nearly sessile cell M_1, and the vein Sc_1 sometimes present. Loss of the discal cell by absence of the medial cross-vein is not uncommon; in fact, the holotype of *walleyi* lacks the medial cross-vein in one wing and has it only faintly indicated in the other. In one specimen, the vein M_3 is basally interrupted, leaving the discal cell open for about half the distance between the junction of M_4 with m-cu and the medial cross-vein. In the vicinity of Ann Arbor, Michigan, there is a population in which individuals having macrotrichia in the outer cells of the wings are not uncommon. Occurrence of this condition in other parts of the range of the species has been noticed, but only in isolated cases.

Males of *walleyi* vary from 9 to slightly over 11 mm. in body length, and their wing measurements range from 9 to 12.5 mm. In the females, the wings are relatively shorter. Body lengths are from 11 to 14 mm., in the specimens examined, while the wings of these measured from about 11 to 13 mm. Larger specimens of both sexes were taken in June, and nearly all the small individuals were from August collections.

There seems to be no particular pattern to the toothed margin of the gonapophyses; that it, within a local population there are as many kinds of margins of gonapophyses as there are gonapophyses. This asymmetry is indicated in Figure 241. In *walleyi*, as in its near relative *similis*, the gonapophyses can be bent backward and ventrally from their bases, and in many specimens this has happened, apparently as a result of muscular action after the flies were placed in the cyanide jar. I have not seen the gonapophyses in such a position in living flies, so I do not know whether this action can be controlled.

In the shape of the tergal arms, there is also great variation (Figs. 64-66), and again there may be dissimilarity between the two tergal arms of one fly (Fig. 238). The depth to which the ninth tergum is cleft varies somewhat in living flies but also varies markedly in specimens preserved dry or on microscope slides, depending on the degree of compression or depression.

Geographical distribution.—The known range of *walleyi* is nearly as extensive as that of *dorsalis* in over-all length and is greater in breadth. The species ranges from Nova Scotia westward to central Alberta, southward to Florida and southwestward to the Ozark Mountains and eastern Kansas. I expect that *walleyi* will eventually be collected in eastern Nebraska and Oklahoma, in Alabama, Mis-



MAP 12. Range of *Dolichopeza (Oropeza) walleyi* (Alexander). Each spot represents one or more collections within a county (United States) or at a locality.

sissippi and Arkansas, and probably in the Turtle Mountains of North Dakota. Its range in Canada is only sketchily indicated; probably it is widespread in moist forests from the Great Lakes to Hudson Bay and northwestward to the Yukon, perhaps even into Alaska. Its occurrence in the Black Hills, where the population may be isolated, is discussed in the conclusions.

Habitats.—Like *obscura,* this species has appeared in a variety of general environments, and because of this wide range of habitat tolerance, *walleyi* is the second most numerous species of *Dolichopeza* in general collections. Common in the vicinity of rocky ravines and gorges, it is also found in many forest situations, where moisture conditions vary from wet to only slightly damp. In Turkey Run State Park, Parke County, Indiana, I regularly found *walleyi* together with the dusky-brown species of the

obscura group in darkened crannies beneath outcropping ledges of sandstone. It was almost as commonly seen suspended among ferns and other leafy plants along the rims of the ravines, where *carolus* was usually found. In narrow ravines through the thick sandstone strata, where there was no accumulation of soil on the ravine floor, hence no trees, few or no low, herbaceous plants, and no mosses (the ravines are rather effectively scoured out by annual spring floods), *walleyi* was not found, although *polita cornuta, tridenticulata, americana* and occasionally some other species were present. This seems to be related to the fact that *walleyi* most often spends its immature stages in mosses that grow on the soil, while the other species mentioned usually pass their larval and pupal stages in mosses that grow on the sandstone cliffs. It is not unusual to collect *walleyi* in upland woods, especially early in the morning. Alexander (1941a: 297), for instance, reported it from rather dry woods at an elevation of 5200 feet, in western North Carolina. I found *walleyi* flitting about in low forest undergrowth atop Spruce Knob, Pendleton County, West Virginia, at approximately 4850 feet elevation, on a very foggy summer morning when the temperature stood at only 49°F. Rogers (1930: 23) records it from ". . . the course of a shaded, rocky, talus slope brook. . . ." in a cove at the edge of the Cumberland Plateau. In Florida, he reared adults from mosses on decayed logs and found other flies of this species among rank herbage on wet, shaded soil (Rogers, 1933: 49). In the southern Appalachian region, *Dolichopeza walleyi* has been found in forest and rocky ravine situations from the piedmont level up to nearly 3000 feet. Whittaker (1952: 34) took *walleyi* in a beech forest; and Rogers (unpublished notes) found it along brooks in wooded localities and about rock outcrops, in the vicinity of Mountain Lake, Giles County, Virginia. Several instances of this fly's having come to or into buildings near wooded areas have come to my attention; and while certain of these structures were picnic shelters and the like, others were buildings in which electric lights were operated at night, such as utility buildings in public campgrounds. Furthermore, there are several records of collection of *walleyi* in light traps, although rarely more than one specimen in any collection. This information, together with repeated daytime observations of *walleyi* spontaneously on the wing over low vegetation in moist woodlands, such as in floodplain forests, suggests that *walleyi* is not as strongly repelled by light as are several other species of *Dolichopeza*.

Occurrence of *walleyi* in swampy woods is not common, although I have occasionally taken it in such habitats together with *obscura* and *subalbipes*, and Rogers (1942:60) noted that the species was ". . . occasionally common in the lower flood-plain woods, birch-maple-elm and tamarack-sumac swamps, and along shaded stream banks; not taken in the marshes where the closely allied *D. sayi* is common, although the habitats of the two species overlap to some extent in the swamps." Only rarely have I taken *walleyi* in marshes; however, in South Dakota, this species was common, together with *dorsalis*, in a marsh of grasses, *Carex*, ferns and sparse, low willow scrub.

Seasonal distribution.—In seasonal distribution, there is again a close similarity between *obscura* and *walleyi*, in that it is somewhat problematical whether there are two annual generations in the area between the southernmost Gulf coast and Florida and northernmost United States and Canada. In his study of the Tipulidae of a southern Michigan locality, Rogers (1942: 60) states that *walleyi* was taken from 28 May to 9 July, in the years 1936 through 1938, with a few records for mid-August of 1938. He concluded that ". . . generally there is only a single generation a year in this region." From my collecting and rearing data, gathered in the same general area, I believe there are two annual generations, the second, however, without as well defined a peak of emergence as the first. In central and southern Indiana, where I have collected a great number of *Dolichopeza*, I have found rather well-marked June and August generations of *walleyi*, the spring peak of abundance coming early in June and the late summer peak around the third week of August. At Turkey Run State Park, Parke County, Indiana, in 1953, *walleyi* males first appeared on 28 May, five days after the first appearance of *polita cornuta* and about two weeks after the onset of emergence of *americana*. By 1 June, the numbers of *walleyi* were still at a low level, but the rise in population seemed to be steady. By 11 July, only a few females were left. The August emergence in this locality was found, in two different years, to be nearly completed by the last two or three days of that month. The Florida records are for March, April and June. In the vicinity of Washington, D. C., there appears to be a June generation and a second flight period from about the end of the third week of August extending into early September. In the northernmost parts of the United States and in the Canadian part of the range, there is a single

generation annually, all the records being for June, July and early August.

Immature stages.—Eggs of *Dolichopeza walleyi* from a female from southern Michigan measured, on the average, .76 by .32 mm. There is no terminal filament. A single female may lay as many as 120 eggs, over a period of three or four nights. In the laboratory one female laid about 110 eggs in two nights but died before laying the few that remained. Hatching began seven days after the first eggs were laid, and many larvae had hatched out by the eighth day.

The larva of *Dolichopeza walleyi* resembles that of *sayi* and, to a lesser degree, that of *similis*. All these larvae have the microscopic hairs of the dorsum most abundant on the last two thoracic and first abdominal segments and on the seventh and eighth abdominal segments, while the transverse ridges are more faintly indicated on the intervening segments. These ridges, in *walleyi* and *sayi*, are readily perceptible, but in *similis* they are extremely faint. The rows of minute microscopic hairs interspersed among the transverse ridges are well defined, about six hairs in length, and about equally spaced in *walleyi*, while they are less well defined, composed of various numbers of hairs, and are crowded toward the transverse ridges in *sayi*.

A larva that I believe is almost certainly this species was described nearly 65 years ago by Hart (1895: 214-215), as a species of *Tipula*. The unknown larva, which Hart called Tipula larva "a," was taken from soil on the floodplain of Spoon River, Illinois. It was regarded as "probably young," very likely because of its small size as compared to other larvae of *Tipula*. Hart described it as follows: "Length 16 mm., diameter 1.5 mm.; grayish, covered with microscopic short dark brown pubescence denser on thorax and last segments, in transverse arrangement; folds very distinct, each slightly tranversely carinate and crested with darker pubescence, four folds on anterior divisions; each segment with the usual four setae, prothorax with several setae. Last segment with lower stigmatal teeth very small, triangularly black on upper surface; upper teeth slender, pointed, whitish, outer pair nearly twice as long as inner pair; a similar tooth anterior to each of the outer two, near the anterior margin of the segment; a blackish spot at the base of each upper tooth, and one below each stigmatal plate; anal prominence with four blunt tubercles about the anal open-

ing." This is the same larva later designated as "*Tipula* sp. 6," by Malloch (1917: 202, pl. 31, figs. 6, 7).

In the shape of the spiracular yoke, *walleyi* pupae rather closely resemble those of *obscura,* but the two species may be readily distinguished by the characteristics of the pleural spinous processes (see key to pupae). Presence of well-developed spinous processes on the posterior ring of the fourth abdominal sternum will aid in recognition of pupae of *walleyi,* as these are found only in a few other species, notably *venosa, subvenosa* and *carolus.* Duration of the pupal stadium is six to seven days, under laboratory conditions. The occurrence of eulophid parasites in this species is described under the natural history of the pupae.

Bryophytes known to serve as microhabitats of the immature stages of *walleyi* are several mosses growing under widely differing moisture conditions. *Atrichum undulatum* is a coarse, often dry moss, usually growing on poor hilltop soil; yet the first immatures of *walleyi* seen were found in this moss. Also fairly dry was the thin mat of *Platygerium repens,* growing on the bark of a fallen tree. In contrast to these were the moist mosses *Amblystegium riparium* and *Mnium affine,* both on the soil at the margin of a temporary, shallow pool in hardwoods, in spring. Other mosses from which larvae or pupae of *walleyi* have been recovered are *Plagiothecium deplanatum, Entodon cladorrhizans,* and *Hypnum imponens,* all of intermediate degrees of moisture and all growing in rather thin mats on forest soil, near streams.

Notes on distribution.—ALBERTA—Bilby (about 30 miles west of Edmonton), 28 June; Fawcett (74 miles north-northwest of Edmonton), 20 June. FLORIDA—Alachua County, 29 March, April, and 3 June; Gadsden County, 5 April; Jackson County, 28 March to 18 April. GEORGIA—Lumpkin Coun'y, 7 June; Union County, 28 June. ILLINOIS—Carroll County, 7 July; La Salle County, 7 July; St. Clair County, 13 August; Vermilion County, 13 June. INDIANA—Jefferson County, 8-9 June and 30 July to 28 August; Jennings County, 3 August; Montgomery County, 28 June; Owen Coun'y, 6-7 and 18 to 26 June, and 3 and 28 August; Parke County, 28 May to 28 June, 11 July, and 28 to 30 August. IOWA—Linn County, 8 July; Winneshiek County, 8 July; Woodbury County, 11 June. KANSAS—Anderson County, 28 July; Douglas County, 25 May, 2 June, and 30 August. KENTUCKY—Barren County, 2 Augus'; Edmonson County, June (?); Franklin County, 23 June; Whitley County, 24 June. MAINE—Cumberland County, 1 July; Hancock

County, 17 July; Oxford County, 11 July; Penobscot County, 25 June to 5 July. MANITOBA—Aweme (20 miles southeast of Brandon), 23 June; West Hawk Lake (near Rennie), 4 August. MARYLAND—District of Columbia, 29 August; Garrett County, 26 June; Montgomery County, 17 to 19 June and 25 August. MASSACHUSETTS—Hampshire County, 27 May. MICHIGAN—Antrim County, 2 July; Berrien County, 17-18 July; Cheboygan County, 22 June to 15 July; Chippewa County, 13 to 15 July; Eaton County, 30 August; Gogebic County, 27 July to 2 August; Iosco County, 28 August; Lake County, 12 June to 1 July; Livingston County, 28 May to 13 June and 14-15 August; Marquette County, 15 to 17 July; Oscoda County, 14 June; Otsego County, 3 July; Presque Isle County, 29 June; St. Joseph County, 12 August; Washtenaw County, 28 May to 29 June and 15 August. MINNESOTA—Blue Earth County, 8 July; Clearwater County, 11 to 17 July; Redwood County, 8 July; Winona County, 7 July. MISSOURI—Barry County, 29 July; Carter County, 6 June; Stoddard County, 31 May; Taney County, 10 June. NEW BRUNSWICK—Fredericton, 26 July. NEW HAMPSHIRE—Coos County, 2 to 11 July; Grafton County, 6 July. NEW JERSEY—Bergen County, 8 to 15 June; Essex County, June. NEW YORK—Broome County, 13 July; Erie County, 19 July; Essex County, 19 June; Hamilton County, 12 July; Herkimer County, 3 July; Niagara County, 23 to 28 June; Rensselaer County, 14 June. NORTH CAROLINA—Avery County, 14 June; Burke County, 14 June; Haywood County, no date; Macon County, 11 June; Swain County, 20 June; Transylvania County, 14 June; Yancey County, 9 to 22 June. NOVA SCOTIA—Halifax County, 5 August; Yarmouth County, 27 June. OHIO—Delaware County, 9 to 14 June; Portage County, 24 June and 14 July; Washington County, 19 June. ONTARIO—Algonquin Park, 26 June to 3 July; Burke Falls, 13 July; Sand Lake (7 miles north of Gananoque, called "Sand Bay" on some maps), 5 July; Thunder Bay (Lake Superior), 9 July. PENNSYLVANIA—Huntington County, 9 July. QUEBEC—Knowlton, 29 June to 12 July. SASKATCHEWAN—Stony Lake (near Humboldt), 5 June. SOUTH DAKOTA—Pennington County (Black Hills), 11 and 23-24 July. TENNESSEE—Blount County, 15 to 17 June; Cumberland County, 25 June; Fentress County, 13 August; Haywood County, 25 May; Knox County, 28 May; Sevier County, 7 to 18 June; Washington County, 30 August. VERMONT—Lamoille County, 17 June; Orange County, 11 July; Rutland County, 12 July. VIRGINIA—Fairfax County, 24 June and 5 September; Giles County, 7 to 22 June and

26 August; New Kent County, 31 May; Rappahannock County, 30 June; Rockingham County, 6 July; Washington County, 18 August. WEST VIRGINIA—Greenbrier County, 4 July; Mingo County, 3 July; Pendleton County, 27 June; Pocahontas County, 23 June; Preston County, 25 June; Tucker County, 24-25 June. WISCONSIN—Jefferson County, 21 June; Trempealeau County, 7 July.

SUMMARY AND CONCLUSIONS

These laboratory and field studies of *Dolichopeza* point out certain problems involving groups of several species and in addition allow a few generalizations that apply equally to all North American species. It has seemed best to discuss these here, in conclusion, following presentation of the detailed data relating to each species.

Taxonomic categories.—It was one of the purposes of this investigation to try to determine what biological species are represented by the various described forms. To do this, it is first necessary to decide what is meant by a species. I visualize a species of *Dolichopeza* as a series of populations of morphologically similar, actually or potentially interbreeding individuals, effectively reproductively isolated from other such series of populations, having a certain geographic range and ecological distribution, and maintaining these characteristics through a span of time in the evolutionary sense.

A satisfactory interpretation of the diversity of structure (and other characters) found in North American *Dolichopeza* requires the examination of large numbers of individuals. Study of one or two specimens here and a few there places undue emphasis on their differences, but when more nearly the full spectrum of variation within a genus can be seen, similarities are emphasized and natural groups can be separated and ranked with perhaps less ease but much more confidence. Individual variants, locally inbred mutations, and geographic races are more likely to fall into their proper taxonomic places when viewed against the background of the entire range of variation of their species. Application of this point of view, I believe, can lead equally to "splitting" or "lumping" of older taxonomic categories.

In judging where specific boundaries should be drawn in *Dolichopeza* (for no matter how ideal his definition of a species, the taxonomist must in the end judge specimens and assign them to specific categories according to his opinion), I have relied heavily on comparative morphology. Individuals having essentially the

same appearance (allowance being made for sexual differences) are presumed to have very similar genotypes and are further presumed to belong to an interbreeding population, if collected in one locality, or to potentially interbreeding populations, if collected in scattered localities. Specific boundaries have been further clarified by the evidence of reproductive isolation among the species recognized. Of the more than 11,000 flies examined, not one was regarded as a hybrid of any two species. Furthermore, among hundreds of mating pairs observed in the field and in the laboratory, none was ever found to involve male and female of different species. Although species of *Dolichopeza* repeatedly come into close proximity under natural conditions and were even caged together in the laboratory, no indication has been found of exchange of genetic materials between species.

Minor variations having more or less random distribution within a species (such as small differences in shape of ninth tergum or minor shifts in position of wing veins), as well as somewhat more striking variations of localized occurrence (for example, locally inbred venational peculiarities) and seasonal size differences, have required no taxonomic recognition. Even in certain cases when variation could be correlated with geographical distribution, taxonomic recognition seemed not to be indicated, such as the instance of *Dolichopeza dakota*, which was judged to be only an extreme in the clinal distribution of color in *D. walleyi*.

Where it has appeared clear that there is gene flow between morphologically distinct forms that are allopatric except for relatively narrow zones of overlap, these forms have been regarded as subspecies, the single example being in *Dolichopeza polita*. Across the zone of contact between the central and eastern forms of this species, in the central and southern Appalachian Mountains, there is concordant change in all the characters that have been found to vary geographically—structure of hypopygium, degree of luster of the thorax, and details of coloration. Individuals of the respective forms from outside the zone of intergradation are in all cases taxonomically distinct and readily separable, but within that zone both forms may occur, together with varying percentages of intermediates. Similar intergradation occurs at the only known locality where the western and central forms meet.

If degree of difference between sympatric species can be taken as a fair indication of the relationship of allopatric forms in the same genus, some support for regarding the subdivisions of *polita*

as subspecies can be gained from the fact that a series of unusual characters common to these very similar forms are not found in any of the other species. Among these are the reversed relative sizes of males and females, the basal enlargement and pointed tip of the outer dististyles in the males, the coiled tracheal connection in the pupa, and the abbreviated terminal filament of the egg.

A series of collections made at Nelson Ledges State Park, Portage County, Ohio, in three different years, included many mating pairs of the eastern and central forms yet never a pair involving both forms and never an individual that could be regarded as an intergrade between the two. Notwithstanding the fact that these two forms intergrade in a zone extending from nearby points in Ohio to eastern Tennessee, in this one locality they may have achieved a specific level of reproductive isolation. Where the eastern form enters Michigan and Wisconsin it is wholly distinct, no areas of contact with the other races having been discovered in that region. An attempt to explain these relationships follows below, under the heading, species formation.

When morphologically distinct forms have allopatric but contiguous geographical distributions yet show no clear evidence of intergradation along the line of contact, as in the case of *Dolichopeza venosa* and *subvenosa*, the forms have been regarded as full species. That these two forms do come into contact has only recently been established, and there is so far no indication of interbreeding, except for the very sporadic occurrence of certain modified characters of each form within the range of the other, as discussed earlier.

In the case of *subalbipes*, where there are two forms with regard to one character only (tergal arm), with continuous gradation in other characters, it seems reasonable at this time to recognize only one species.

Isolating mechanisms.—In *Dolichopeza*, closely related species often have nearly identical geographical ranges and are often the most closely associated ecologically. There is some very general environmental segregation, yet adults of as many as half a dozen species may not infrequently occur so close together in their daytime resting places that they come into physical contact, especially when in swarming flight following some disturbance. Larvae of two or three species are occasionally found within a patch of a single species of moss no larger than the palm of one's hand. Under such circumstances, it is difficult to imagine how these species might

be separated by any environmental barriers. Of course, isolation in any stage but the adult is irrelevant to the problem of interspecific isolation; we are concerned here with reproductive isolation, which must be complete in the case of sympatric sibling species in order for them to retain their identity. Reproductive isolation ordinarily occurs because males and females of different species are not attracted to each other and thus do not mate at all. In other instances in which mating between species does occur, either there may be no fertilization or, if fertilization is accomplished, the offspring may be either inviable or sterile. The composition of mating pairs mentioned earlier suggests that in *Dolichopeza* the first of these possibilities is the rule.

Differences in size of individuals and in relative proportions of genitalic structures could probably account for a certain amount of isolation between species in the same habitat, as between *similis* and *dorsalis,* but in most cases I cannot see any structural barriers to interspecific matings. As pointed out earlier, there is no "lock and key" arrangement in copulation. The fact that peaks of emergence of adults do not coincide may provide a degree of reproductive isolation, but there is still such great overlap in the seasons of emergence of the various species in any locality that this would scarcely seem to be an effective isolating mechanism. It has been noted that mating in *americana* often takes place by day, while species of *Oropeza* ordinarily mate at night. This, however, fails to explain isolation among the closely related species of *Oropeza,* which is really the problem at hand.

That species of *Dolichopeza* carry on mating and other activities primarily in the hours of darkness may still have some bearing on the means of isolation. It seems not unlikely that the process by which males and females of one species are attracted or brought together might also serve to repel all other species. That is, each species might be characterized by a particular odor, allowing males to detect females of their own species and distinguish them readily from all others. Flies caged in the laboratory, as well as those congregated in natural resting sites, occasionally exhibit diurnal mating but in general ignore one another, by daylight, unless they come into bodily contact. It is possible that matings begun in daylight hours are merely the result of reflex reactions following appropriate but accidental contacts and that the stimulus of daylight causing resting behavior ordinarily overcomes any stimulus for other activity short of actual contact.

Population control.—Potentially, a local population of any species of *Dolichopeza* could saturate its environment in a short while; however, it is my general impression that, in areas where I have made observations over a period of several years, such local populations have remained about the same. It is, of course, difficult to discover whether populations of various species of *Dolichopeza* are in the long run increasing or decreasing. It seems not unreasonable to assume that, although each species is constantly striving to increase, any particular population fluctuates from year to year according to environmental factors and that net gains during a favorable year may be wholly or in part cancelled by losses in an unfavorable one.

The number of individuals of a species in a local population (and it is both reasonable and convenient to think of species of *Dolichopeza* in terms of many localized, partially isolated populations) is derived from an interaction of the species' potential rate of reproduction and the effects of the environment. Each female reaching the adult stage is presumably capable of depositing 100 to 120 eggs. The longevity of ovipositing females needs to be taken into account, although most of the eggs seem to be laid within three or four days of the time of emergence. One must also consider, in connection with the species' reproductive potential, the number of generations per year. Assuming for simplicity that there is but one generation each year and that the population shows no measurable increase from year to year, it may be seen that 98 percent or more of the potential offspring of each generation are lost before the next. What is the fate of all these individuals?

Due probably to the method of fertilization, as many as a third of the eggs of one female have been observed, in the laboratory, not to hatch and are assumed to have been infertile. The proportion of such losses in nature cannot easily be estimated, but it is difficult to imagine biological perpetuation of such inefficiency. Mortality in the larval stages has been found to result from predation, parasitism, disease, and the effects of severe adverse weather, such as excessive rainfall, drouth, or extreme temperatures. In the laboratory, many individuals died in the pupal stage, from predation, parasitism and unknown causes. Of the adults that survive the hazards of emergence from the pupal skin, certainly many do not reproduce, again by reason of predation, disease, weather or accidents of one sort or another.

Other environmental limitations that need to be considered are

availability and quality of food, space in the habitat, and competition—both among individuals of the same species and among the various species inhabiting the same general environment—for food and space.

Competition.—There is no evidence of competition among species of *Dolichopeza*, either from records of changes in species composition in various localized environments, over the years, or from field observations of many larvae and numerous large aggregations of adults. In habitats where a number of species are present, there seems always to be more than enough of both the bryophyte microhabitats for the immature stages and shaded resting places for the adults. As mentioned earlier, the moss or liverwort habitat is almost never fed upon by the larvae sufficiently to cause readily visible damage. Even though larvae of three species may be feeding together in one kind of moss, they rarely come into contact with each other because of the abundance of the moss (which is at once their food and shelter) and because individuals were initially spaced within the habitat as a result of the method of oviposition.

It might be theorized that, in time, one species or another, by being more exactly adapted to the environment, would so gain in numbers as to force the others out through competition. However, it seems probable that fluctuations in the environment favor first one species and then another and that, because of the irregular geographical distribution of such fluctuations, a species may gain temporary predominance in one locality but fall to low numbers in another, in an ever-changing pattern. As Ross (1957: 127) points out, "Because no two species are exactly alike genetically and therefore physiologically, each species should theoretically have an ecological optimum slightly different from all other species. It follows that, in cases of multiple occupancy of a niche [by species of the same genus], each species will tend to become abundant at a time or place different from the other species."

It appears that numbers of *Dolichopeza* are so reduced by predation, parasitism, disease and rigors of the physical environment that competition, except perhaps at the level of the individual, never comes into play as a force in population control. Absence of competition, either among species of *Dolichopeza* or between this genus and species of *Liogma, Tipula,* etc., living in the same habitat, would furthermore seem to be an important factor in the ability of several species of *Dolichopeza* to occupy one and the same ecological niche.

MAP 13. Some ecological factors influencing the distribution of *Dolichopeza* in North America. Shading indicates forested regions; heavy lines are isophenes of average length of frost-free period, in number of days indicated.

Geographical distribution.—In a general way, the pattern of distribution of the genus *Dolichopeza* in North America corresponds with that of the forests in the eastern and subarctic regions of the continent (Map 13). Within this vast area, there are many recognized forest types, and one species of *Dolichopeza* may range through several of these. Accordingly, the composition of the forest does not appear as important to the distribution of these crane flies as the general effect that the presence of forest trees has upon the microhabitats required by the flies and their larvae. So similar are the ecological needs of species in various groups of *Dolichopeza* that the geographical ranges of certain of them nearly coincide. In fact, if the known ranges of all species were outlined on one map, it would be seen that the area including roughly the Great Lakes basin and the northern Appalachian Mountains is inhabited by twelve of the fifteen recognized species. A series of zones drawn around this central area would include diminishing numbers of species toward the periphery of the range of the genus. Even near the periphery, however, any habitat suitable for one species is likely to support two or more. Thus, in eastern Kansas, near the western limit of the forests, were found *obscura, polita pratti* and *walleyi;* of two specimens of *Dolichopeza* taken in the Ouachita Mountains on the border between Arkansas and Oklahoma, one was *johnsonella* and the other *tridenticulata;* and in western Alberta, near the Continental Divide, over which no species seems to have passed, at that latitude, were found *americana, dorsalis, obscura* and *walleyi.* On the other hand, the range of every species must naturally come to an end somewhere, and I certainly do not suppose that, at the actual outer limits of the range of the genus, at least two species will always be found existing in the same habitats. Beyond the region of generally satisfactory habitats, perhaps one species here and another there may be pioneering, as it were, various marginal environments. Each species probably expands its range during years in which its over-all environment has been most nearly optimum, only to be thrown back in unfavorable years, perhaps here and there holding some of the gained ground in spite of adversity.

Although there seem to be altogether favorable habitats for *Dolichopeza* in the luxuriant forests of the Cascade Range of Oregon and Washington, the genus has apparently been prevented from westward expansion at this latitude by the Great Plains. By the route of the subarctic forest, several species occurring in eastern

North America have spread northwestward across Canada toward Alaska, bypassing the treeless plains and even moving a little way southward again, below the eastern slopes of the Rocky Mountains, following an extension of the boreal spruce-fir forest. So far as is known, however, these species have not penetrated the western coniferous forest (lodgepole pine, western yellow pine, etc.) and remain east and north of the Continental Divide.

If the plains are such an effective barrier to the spread of *Dolichopeza,* how does the genus happen to be represented by at least three species in the isolated Black Hills of South Dakota? One might at first suspect a connection to the main eastern range by way of the valleys of the Missouri and Cheyenne rivers, yet there is a 300-mile gap between the Black Hills and the northwestern extremity of oak-hickory forest in the Missouri Valley. The species composition of the Black Hills group (*americana, dorsalis* and *walleyi*) suggests that the group's geographic affinities are with the area to the north; however, once more the continuity of habitats is widely broken. It seems that the Black Hills are in fact wholly isolated and that species of *Dolichopeza* now living there have no connections whatsoever with their main eastern and northern ranges. In order to account for this distribution, it is necessary to visualize that at the time of maximum extent of the last (Wisconsin) continental glaciation, *Dolichopeza* occupied a forest that grew all along the ice front, which is to say from the Rocky Mountains along the Missouri and Ohio rivers to the Appalachian Mountains. As the ice withdrew northward, followed by the boreal forest, a remnant of that forest, into which elements of the Rocky Mountain forest had become introduced, was left behind, where, because of the cooler climate and higher rainfall in the isolated mountains, it withstood the encroachment of drier forests and eventually of grasslands. If this is how species of *Dolichopeza* came to be in the Black Hills today, what accounts for their not having visibly changed from the parent stocks in their ten thousand years or more of isolation?

The species involved all have unusually extensive ranges, spanning approximately thirty degrees of latitude and including habitats from near sea level to more than 6000 feet elevation, distributed in a great arc nearly 4000 miles long from southeastern United States to northwestern Canada and Alaska. Not one of them, however, has differentiated into geographic races in response to the great ecological diversity encountered within its range. This suggests that these species have a high degree of adaptability and

that such changes in genetic constitution as have been necessary to adapt physiology to environment have been so small that they have not become manifest in the phenotypes. It is thus not unusual that species of such constitution have remained essentially unchanged through ten thousand years in isolation, for surely the environment has changed less in the Black Hills during that span of time than it changes today over the length and breadth of the described range.

Seasonal distribution.—The geographic range of the genus *Dolichopeza* in North America may be divided into three major zones with respect to seasonal distribution. These are: (1) Florida and the extreme southern Gulf Coastal Plain, where emergence of adults may occur in almost any month of the year; (2) a broad middle belt extending from Florida and the Gulf Coast area northward to New England, central Michigan and southern Wisconsin and Minnesota, in which there are normally two annual appearances of adults, falling roughly in June and August; and (3) a northern zone, in which one annual flight period, usually during late June and July, is the rule. As this pattern of seasonal occurrence correlates in general with latitude and since cold weather is known to inhibit feeding activities of the larvae, temperature appears to be the chief factor involved.

Duration of the frost-free season may perhaps be taken as a measure of the time available for larval feeding and growth, hence of the potential production of adults. If contours are drawn upon a map, connecting points of equal average duration of frost-free period, two of these contours very closely approximate the zonal boundaries of seasonal distribution in *Dolichopeza*. The boundary between the southern and middle zones falls near the 260-day contour (Map 13), and the middle and northern zones are separated more or less along the 150-day contour. On the average, the last frost of spring along the southern contour is in early March and the first frost of fall in late November or early December. Along the northern contour, the last spring frost is usually around mid-May, while the first in autumn comes in early October. Within the broad middle zone, there is thus an average feeding and growing season of somewhat over 200 days. Rearing of *Dolichopeza sayi* in southern Michigan indicates (Fig. 99) that about 70 days are required for the development of one generation. Accordingly, supposing that occurrence of frost brought larval feeding and growth to a halt, there would be only sufficient frost-free days at

that latitude to produce two generations of *sayi* in an average year. It is furthermore not unlikely that when frosts come early in the fall or persist late in spring, only one generation may be produced, as in the northern zone. Depending on local micro-climates, there may result a partial second generation, which would perhaps account for the fact that, in the northern part of the middle zone, the number of adults in the late summer generation is often conspicuously smaller than the number seen at the same locality during the spring emergence.

Species formation.—Dolichopeza is probably a very old genus. The present day tipuline genera *Brachypremna, Tipula, Ctenophora* and possibly *Nephrotoma,* as well as nearly twenty modern genera of the Limoniinae, were already differentiated in Oligocene time (see Alexander, 1931d) and are represented as fossils in deposits of that epoch in Europe and North America, especially in the Baltic amber. As *Dolichopeza* is regarded as a rather primitive genus among the Tipulinae, it quite possibly was differentiated prior to the Oligocene and spread widely into North America from Asia, at a time when a low, forested land connection existed between the two continents in the region of Alaska.

There appear to have been three, possibly as many as five, separate introductions: one or two each of *Dolichopeza* s. s. and *Oropeza* and one of *Megistomastix,* a West Indian subgenus that seems not to have been derived from either *Oropeza* or typical *Dolichopeza.* Given the forty million years or so, suggested above, to diversify in North America, these originally introduced species could easily have given rise to the present fauna, notwithstanding their apparently slow rate of evolutionary change. Despite the evident ability of species of *Dolichopeza* to adapt to diverse general environments, it seems likely that the fifteen species present today are all that remain of a sometimes greater or sometimes lesser number of predecessors, many species having arisen and later become extinct since the original introduction of the genus into this continent.

Species formation has, I believe, resulted from effective spatial isolation. It is not difficult to imagine that during the geological past there were, as there are today, portions of the ranges of species in which populations are partially or altogether isolated. It is plain from the above studies that different genotypes may build up even in various parts of the more or less continuous range of a species, probably due to low vagility of the flies. Depending upon

the degree of isolation, adaptive and non-adaptive changes that arise by mutation in such populations will be either slowly diffused into the genotype of the entire species or retained locally. Changes mixed into the genetic composition of the species as a whole may become lost completely or may persist as intraspecific variation. If locally occurring changes are advantageous (that is, have some small survival value), they may alter the entire parent species by outward diffusion from the place of origin, or, if long enough isolated, they may give rise to new species.

Differentiation of most of the existing species of *Dolichopeza* must have occurred at a time so remote that one could only speculate in general terms how or where it came about. If, however, one regards geographic races as incipient species, the case of *Dolichopeza polita* may be instructive. Much of the present range of this species lies in the area occupied by the last Pleistocene continental glacier; therefore, if the species existed at the time of that glacial advance, it must have been forced southward, into the Ozark Mountains, the central and southern Appalachian Mountains and part of the broad intervening lowland. If the habitats of the species have not changed appreciably, then the Ozark population (*polita pratti*) must have been rather effectively isolated by the lower Mississippi Valley, in which rock outcrops are not common; and the eastern and central populations probably were partially isolated on the eastern and western slopes of the Appalachians, respectively. Following the withdrawal of the glacier, the Ozark and central forms could have slowly made their way northward through the advancing forests, from one rocky or outcrop area to the next, not coming into contact until they reached north central Illinois. The central form (*polita cornuta*) maintained its subspecific relationship with *polita polita* along the Appalachian ridges but on reaching northern Ohio encountered representatives of the typical race moving westward from Pennsylvania, from which area the central form had long been isolated by the glacier. There the two forms reacted as full species. The eastern form, meanwhile, being less restricted to rocky habitats and proceeding from an unglaciated area much farther north than the other two, moved westward through the Great Lakes region until it encountered *polita cornuta* in Michigan and *polita pratti* in Wisconsin, in each case failing to interbreed and thus maintaining a specific degree of isolation. This interpretation is based upon present knowledge of distribution (see Map 6) and, of course, may need to be changed when further data are available.

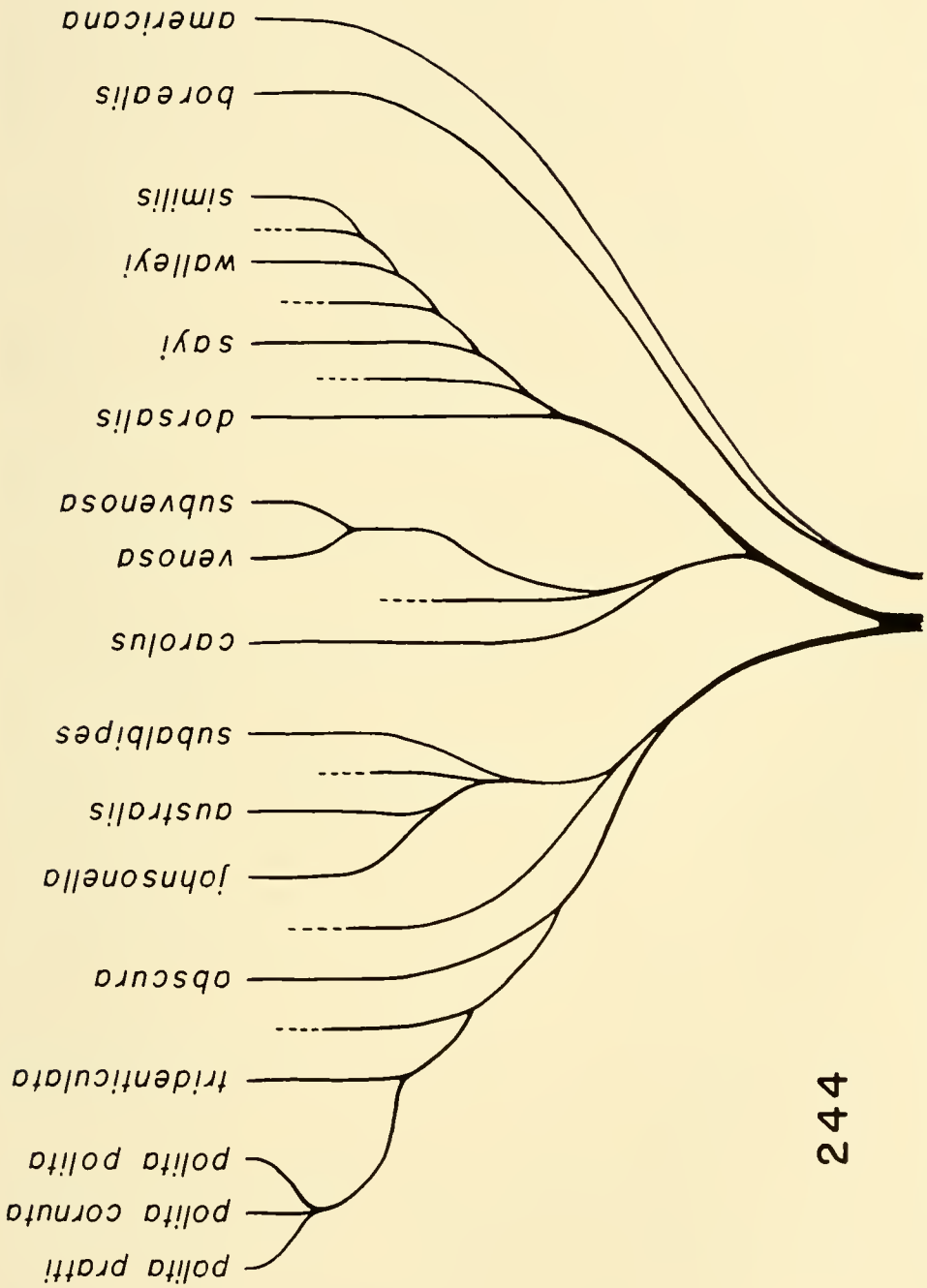


FIG. 244. Diagram of supposed relationship of species and subspecies of the genus *Dolichopeza* in North America.

Interspecific relationships.—It seems likely that within the genus *Dolichopeza* certain adaptive structures have become well established and might be thought of as having reached a degree of stability as a result of close correlation of form with function. Stated another way, it may be that the genus must retain these characteristics in order to survive in its particular range of ecological niches. These characters common to all species of the genus may be said to be primitive for the genus, although they may be specialized in comparison to common characters of the family Tipulidae. Applying this same principle to the arrangement of species within the genus, widespread characters such as the pattern of wing venation may be regarded as primitive at the subgeneric level, or a certain kind of gonapophyses as primitive for a species group. Thus, the more characters any two species have in common, the more closely related they are judged to be. In attempting to arrange the species according to their most probable relationships (Fig. 244), I have used wherever possible characters least likely to have been directly influenced by environment. Hypopygial features, for example, have been found most useful, for I cannot perceive that the variations in shape of the ninth tergum, the dististyles or gonapophyses would be affected materially by a change in the species' environment. In contrast, coloration seems to be closely correlated with the type of habitat. On the basis of coloration, *subalbipes* would appear more closely related to *carolus* than to *johnsonella,* and *walleyi* more closely akin to *dorsalis* than to *sayi.* The various relationships indicated in Figure 244 are discussed in detail in the species accounts and need not be repeated here. Although this figure indicates no time scale, the levels of separation of lines of descent are intended to suggest relative lengths of time. The presence of most species both within and outside the area of the last Pleistocene glaciation suggests they have existed for approximately 10,000 years, at least. Lines of descent terminated by dashes are introduced to indicate supposed indirect derivation of one existing line from another. Lastly, considering only those characteristics of larvae and pupae used in this study for differentiating species, it appears that differences in the immature stages are of phylogenetic significance rather than adaptations to environment.

A brief hypothetical history of the genus Dolichopeza in North America.—The distribution of North American species of *Dolichopeza* indicates that they are a boreal and sub-boreal group, vir-

tually limited to forested areas. In the Oligocene, the genus *Dolichopeza* may have been widely distributed in the northern parts of Europe, Asia and North America, for cool forests are thought to have been widespread in the northern continents, at that time. As a result of subsequent cooling of continental climates, this forest belt was displaced southward, carrying with it its fauna; and in early Miocene time, the genus *Dolichopeza* possibly occurred throughout much of its present North American range, as well as in much of the western part of the continent. With the renewed uplift of the present Rocky Mountains, during the Pliocene epoch, the western forests were widely obliterated, giving way to grasslands in the rain shadow area east of the mountains and being somewhat replaced in the far west by a new flora of conifers. *Dolichopeza,* now confined to the hemlock-hardwood and deciduous forests of eastern North America, was widely separated from the Asiatic stock. Advances and recessions of Pleistocene ice forced some components of the genus as far southward as the Gulf coast and probably caused fractions of the populations of various species to become isolated, giving rise to new forms. With the last retreat of the continental glaciers, most of the populations drifted northward into the newly developing forests, but some stayed behind in the more deeply-shaded swamps and cooler valleys of the South. As the land warmed and oak-hickory forests replaced the moister woodlands, fragments of the once widespread populations of *Dolichopeza* were left in the cool ravines and valleys of the Mississippi basin, together with relict stands of the hemlock-hardwood forest. Today, the stronghold of *Dolichopeza* is in the forests of the upper Great Lakes, St. Lawrence and New England regions, and in fragments of that forest extending southward along the crests of the Appalachian Mountains. From this area, some species have moved far northwestward through the subarctic spruce-fir forest, finding there environmental conditions adequate for their needs. Outside the spruce-fir and hemlock-hardwood forests, however, the present discontinuous pattern of distribution is, in a sense, a slowly fading ghost of what once was probably the center of concentration of the genus *Dolichopeza* in North America.

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Summary of Fossil Microfloral Investigations in the Bevier, Weir-Pittsburg, Lower Williamsburg and Blue Mound Coals of Eastern Kansas

BY

SAM L. VAN LANDINGHAM

ABSTRACT: The following report concerns the identification and description of microflora of the Bevier and Weir-Pittsburg Coals (Des Moinesian Series of Pennsylvanian System) and the Lower Williamsburg and Blue Mound Coals (Virgilian Series of Pennsylvanian System). No attempt is made to correlate any coal beds. This is simply a preliminary report dealing with some of the many types of plant cuticles and other types of plant microfossils present in the Cherokee and Douglas Group Coals. I feel that much more work should be done before any attempt at correlation on a broad scale is attempted.

INTRODUCTION

The following presentation was done with the aid of a National Science Foundation Research Grant, under the direction of Dr. R. W. Baxter, Department of Botany, University of Kansas, and constitutes part of a general study of the coal-age flora of eastern Kansas.

The samples studied are described as follows:

Sample 19: Bevier Coal from core sample from Mack Colt Oil Company No. 14a Colt-Alexander; 1.95 feet long, extracted from a depth of 994.85 feet; from NW¼ SW¼ Sec. 9, T. 23 S., R. 18 E., Anderson County, Kansas; "a" is bottom portion of sample, "b" is middle part and "c" is top.

Sample 7: Weir-Pittsburg Coal from NE Sec. 24, T. 32 S., R. 23 W., Cherokee County, Kansas; "a" is lower 2 feet, "b" is middle 1.5 feet and "c" is top 1.3 feet.

Sample 6: Weir-Pittsburg Coal from Sec. 7, T. 33 N., R. 33 W., Barton County, Missouri; "a" is lower 10 inches, "b" is middle 10 inches and "c" is upper 10 inches.

Sample 4: Weir-Pittsburg Coal from Blue Ribbon Mine in Sec. 25, T. 29 S., R. 25 E., Crawford County, Kansas; "a" is lower portion, "b" is middle portion and "c" is upper portion.

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Blue Mound: Blue Mound Coal from NE¼ of NW¼ of Sec. 28, T. 13 S., R. 20 E., Douglas County, Kansas; site was approximately 100 feet NE of the Coal (Cole) Creek Bridge on the north side of the Creek. (Plate 29.)

Lone Star Lake: Lower Williamsburg Coal? from NW corner Sec. 13, T. 14 S., R. 18 E., Douglas County, Kansas; outcrop thickness below the Lone Star Lake Spillway was approximately 18 inches of coal and carbonaceous shale; bottom sample included lowermost 5½ inches, middle sample included next 2 inches and upper sample included next 3 inches (see plate 29). The bottom sample was coal, and the middle and upper samples were coal and carbonaceous shale. (Plates 26-28.)

The sample numbers correspond to slide numbers mentioned on plates 1-30. Most of the slides mentioned on plates 1-30 are on file with Dr. R. W. Baxter: Department of Botany, University of Kansas, Lawrence, Kansas.

PREPARATION OF SLIDES

The coal samples were washed and crushed to particles approximately one cm. in diameter and placed Schulze's solution (saturated aqueous solution of $KCLO_3$ plus two or three parts of cold, concentrated HNO_3). After approximately 24 hours in the Schulze's solution, the samples were washed and siphoned six times, allowing one and one-half hours for each settling between siphonings. The samples were then placed in a 7% KOH solution and allowed to remain for one hour. They were then washed and siphoned eight times, allowing two hours for each settling between each siphoning. The samples were separated through a 625 micron (40 meshes per inch) screen. The smaller fraction (– 625 microns) was placed in successive alcohol baths of 5, 10, 25, 50, 75 and 95%, each for a total of 30 minutes. The treated samples were stored in absolute alcohol. Small amounts of the samples were placed on glass cover slips. Diaphane was then added, and this mixture was spread over the glass slip and allowed to dry. Balsam was then applied to a glass slide, and the glass slip was placed on the balsam. No staining was attempted. The larger fraction (+ 625 microns) was dried and examined for megaspores (mainly *Triletes*). The large spores were mounted in cardboard microslides. The cuticles were hand picked from the larger fraction and mounted with balsam. Some of the larger pieces of cuticle were hand picked from the samples and treated with household bleach for 154 hours until all of the debris was removed.

TENTATIVE LIST OF PLANT MATERIALS IN BEVIER, WEIR-PITTSBURG, LOWER WILLIAMSBURG AND BLUE MOUND COALS

The following lists are arranged in order of decreasing importance. Both frequency of occurrence and total bulk were taken into consideration. Cuticles with unknown affinities are not included in these listings. In every case the Cordaitales were most important.

Bevier Coal, Plates 2-10, 22

1. Cordaitales
   - *Cordaites*-type fragments (abundant)
   - *Florinites* (common)
   - *Cordaianthus* fragments (rare)
2. Lepidodendrales
   - *Lepidodendron*-type fragments (abundant to common)
   - *Lycospora* (abundant, most frequent microspore)
   - *Triletes* (rare)
3. Spores *Incertae sedis*
   - *Punctatosporites* (abundant)
   - *Laevigatosporites* (common)
   - *Latosporites* (common)
   - *Verrucososporites* (sparce)
   - *Triquitrites* (sparse)
   - *Anapiculatisporites* (sparse)
   - *Schopfites* (rare)
   - *Leiotriletes* (rare)
   - *Vestispora* (rare)
4. Filicineae (ferns)
   - *Punctatisporites* (abundant)
   - *Granulatisporites* (rare)
   - *Raistrickia* (rare)
5. Calamitales
   - *Calamospora* (common)
6. Medulloseae (and other seed ferns)
   - *Monoletes* (common)
   - *Medullosa*-type fragments (rare)
   - *Dolerotheca?* (rare, only one fragment was found)

Weir-Pittsburg Coal, Plates 2-5, 9, 10, 23

1. Cordaitales
   - *Cordaites*-type fragments (abundant)
   - *Florinites* (abundant)
   - *Endosporites* (common to abundant)
   - *Cordaianthus* fragments (rare)
   - *Pityosporites* (rare, only two were found)

2. Lepidodendrales
   Lepidodendron-type fragments (common to rare)
   Lycospora (common)
   Triletes (common)
3. Filicineae (ferns)
   Punctatisporites (abundant)
   Granulatisporites (rare)
   Raistrickia (rare, only one was found)
4. Medulloseae (and other seed ferns)
   Monoletes (common)
   Medullosa fragments (rare)
5. Calamitales
   Calamospora (rare)

Lower Williamsburg Coal, Plates 11-21, 24, 25

1. Cordaitales
   Cordaites-type fragments (abundant)
   Cordaianthus fragments (abundant)
   Florinites (abundant)
   Endosporites (abundant)
   Wilsonia (rare)
2. Lepidodendrales
   Triletes (abundant) (some may be related to *Sigillariostrobus*)
   Lepidodendron-type fragments (common)
   Lepidocarpon megaspores (common)
   Lycospora (common to abundant)
3. Spores *Incertae sedis*
   Triquitrites (common to abundant)
   Laevigatosporites (common to abundant)
   Reticulatisporites (common)
   Latosporites (common)
   Leiotriletes (common to rare)
   Microreticulatisporites (common to rare)
   Pustulatisporites (rare)
   Cyclogranisporites (rare)
   Vesicaspora (rare)
   And etc.
4. Filicineae (ferns)
   Punctatisporites (abundant)
   Granulatisporites (common to rare)
   Raistrickia (rare)
5. Calamitales
   Calamospora (common)
6. Medulloseae (and other seed ferns)
   Monoletes (common)
   Neuropteris fragments (rare) (mainly *N. scheuchzeri*)
   Medullosa fragments (rare)

Blue Mound Coal, Plates 11-16, 21

1. Cordaitales
   Cordaites type fragments (abundant)
   Florinites (abundant)
   Endosporites (common to abundant)
   Cordaianthus fragments (rare to common)
2. Lepidodendrales
   Triletes (abundant) (some may be related to *Sigillariostrobus*)
   Lycospora (common to abundant)
   Lepidodendron type fragments (common)
   Lepidocarpon megaspores (rare)
3. Spores *Incertae sedis*
4. Filicineae (ferns)
   Punctatisporites (abundant)
   Granulatisporites (common to rare)
   Raistrickia (rare)
5. Calamitales
   Calamospora (rare to common)
6. Medulloseae (and other seed ferns)
   Monoletes (common)
   Medullosa type fragments (rare)

CONCLUSION

Coal is a natural occurrence, and strata are natural occurrences. Fossils also occur naturally. All plant fossils must be studied from a natural standpoint in order to obtain a natural reconstruction of the past. The artificial method of studying plant microfossils is that method by which spores and other plant fragments are used for correlative purposes with little or no consideration of the plants from which they came. Any artificial approach to the study of plant fossils produces an artificial picture and also an *incomplete picture of the past.* The artificial method is perhaps the most efficient, but the most efficient method is not always the best method.

Much of geology and paleontology is based upon the phrase "The present is the key to the past." The present is natural, not artificial. Is it not a logical procedure to interpret the natural present in terms of the natural past?

This short paper is an attempt at the *natural* approach to the study of plant microfossils. One good natural procedure is to use the spores to determine stratigraphic position, the associated cuticles and other fragments to correlate these stratigraphic positions, and the cuticles and spores together to determine and recon-

struct the plants from which they came. The reconstructed plant is the key to the environment. A great deal more work must be done before a procedure of this type would be possible.

Fossil spores are very useful in determining the stratigraphic positions of coal samples, but in correlating several coal samples, the amounts of the various spore genera and species vary from sample to sample. Plant cuticle types are usually present in fairly consistent amounts from coal samples of the same age. In many cases fossil plant cuticles and other tissues exclusive of spores are much better to do correlative work with than spores. A person needs only to look at Wilson and Hoffmeister's (1956) cuticle histograms on plate 2 of that paper to see this.

A better understanding of fossil plant cuticles associated with fossil spores would mean a better, more natural, and more complete understanding of the past than the now popular artificial system gives us.

ACKNOWLEDGMENTS

I thank Dr. R. W. Baxter for his aid and assistance. Also, thanks to Arthur Cridland and John Morris for critical evaluation. I am also grateful to Al Hornbaker and Dan Habib of the Kansas Geological Survey for their help on the Bevier and Weir-Pittsburg Coals.

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PLATE 1

FIG. 1. Idealized stratigraphic column of Southeastern Kansas showing position of Cherokee Group coals (Des Moinesian Series of Pennsylvanian System). One inch equals approximately 45 feet.

FIG. 2. Idealized stratigraphic column in Douglas County, Kansas, showing position of Douglas Group coals (Virgilian Series of Pennsylvanian System). One inch equals approximately 120 feet.

PLATE 1

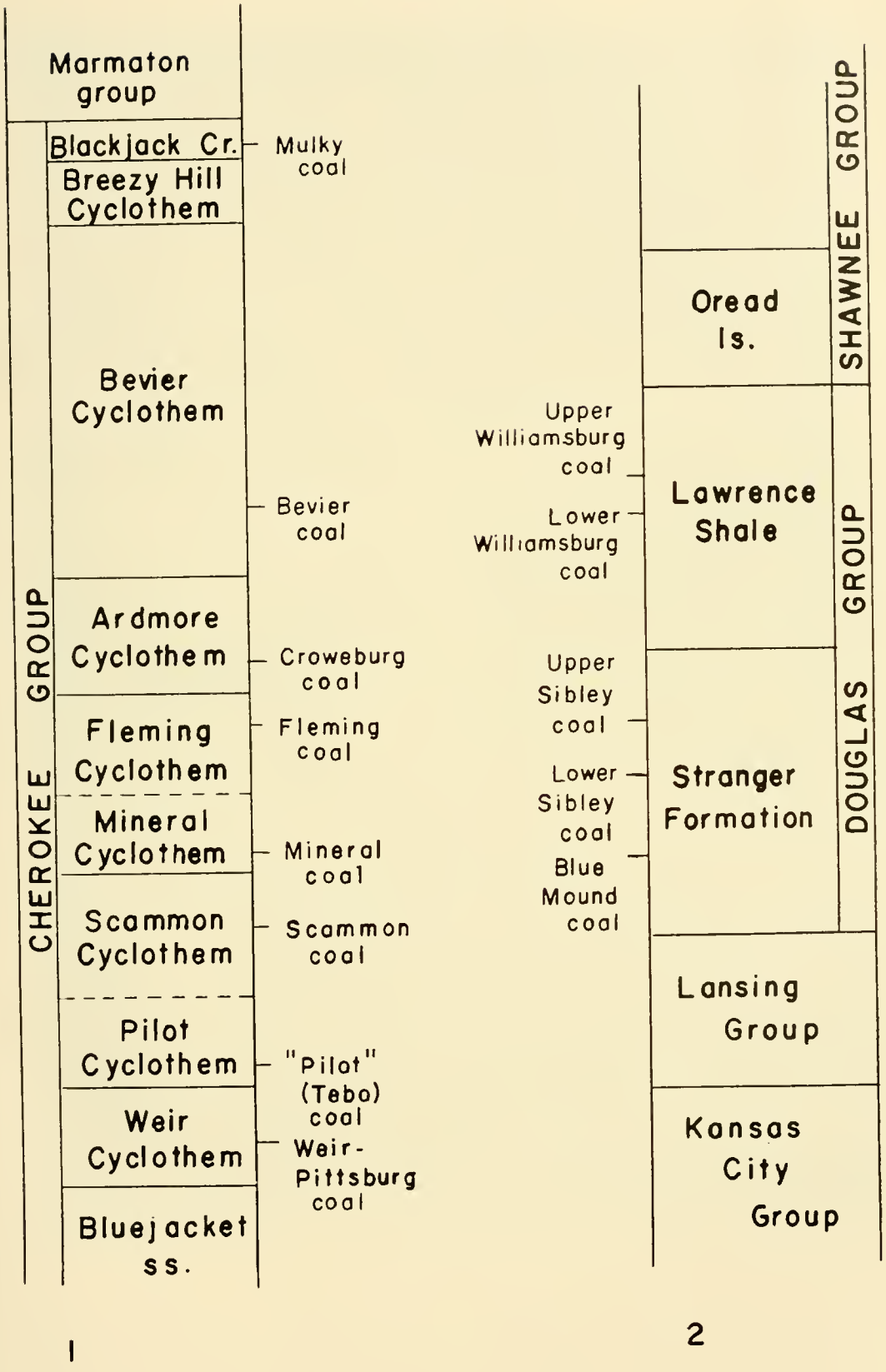

Marmaton group
CHEROKEE GROUP
Blackjack Cr.
Breezy Hill Cyclothem
Bevier Cyclothem
Ardmore Cyclothem
Fleming Cyclothem
Mineral Cyclothem
Scammon Cyclothem
Pilot Cyclothem
Weir Cyclothem
Bluejacket ss.
Mulky coal
Bevier coal
Croweburg coal
Fleming coal
Mineral coal
Scammon coal
"Pilot" (Tebo) coal
Weir-Pittsburg coal
1
Oread ls.
SHAWNEE GROUP
Upper Williamsburg coal
Lower Williamsburg coal
Lawrence Shale
Upper Sibley coal
Lower Sibley coal
Blue Mound coal
Stranger Formation
DOUGLAS GROUP
Lansing Group
Kansas City Group
2

PLATE 2

FIG. 1. Longitudinal view of *Lepidodendron* scalariform tracheid of primary xylem; common in Bevier Coals, especially in upper levels; not common in the Weir-Pittsburg Coal; Slide 19a No. 2, Bevier Coal; × 59.

FIG. 2. Enlargement of area framed in black on figure 1; note fimbrils ("threads") extending across pit openings (white arrow); × 271.

FIG. 3. Tracheids of Cordaitean affinities; common in both Bevier and Weir-Pittsburg Coals; Slide 19a No. 2, Bevier Coal; × 59.

FIG. 4. Enlargement of area framed in black on figure 3; × 271.

FIG. 5. Tracheids probably associated with some Cordaitean-type plant; pits are elliptical-shaped and in some of the tracheids there are only two or three rows of pits while in others there are as many as seven rows; common in Weir-Pittsburg Coal samples; Slide 6a No. 4, Weir-Pittsburg Coal; × 59.

FIG. 6. Enlargement of area framed in black on figure 5; × 271.

PLATE 2

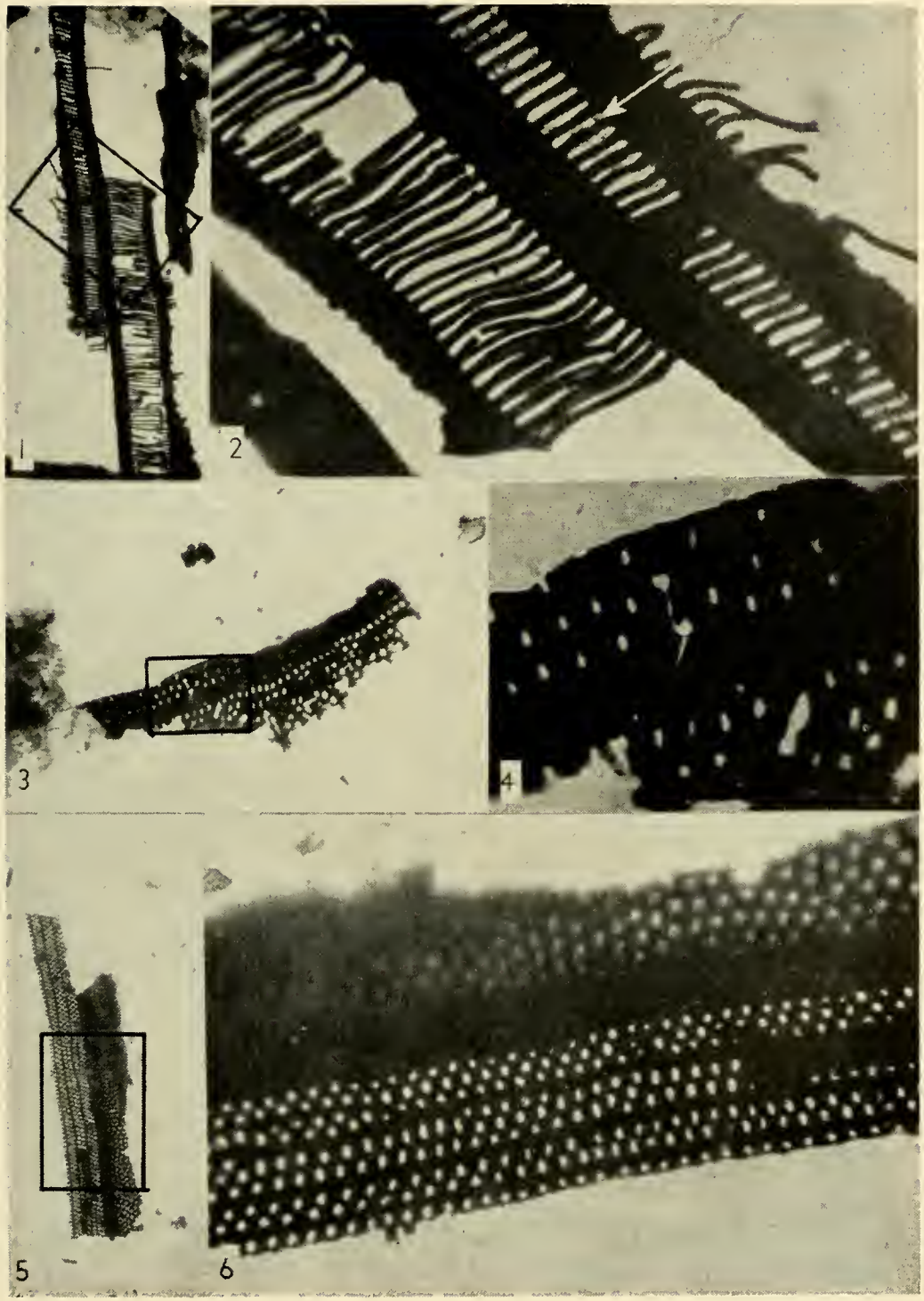


PLATE 3

FIG. 1. Wood fragment from the transition between primary and secondary xylem of *Cordaites?* tracheids; (*Cordaites* metaxylem with large spiral tracheids?); fairly common in the Weir-Pittsburg samples; Slide 4c No. 36, Weir-Pittsburg Coal; × 271.

FIG. 2. Tracheid of *Lepidodendron;* note fimbrils (white arrow); Slide 19a No. 2, Bevier Coal; × 271.

FIG. 3. Wood fragments of Cordaitean or Lycopodian affinities; upper left —*Cordaites?* scalariform tracheids; center—*Cordaites?* metaxylem with spiral tracheids; common in Weir-Pittsburg and Bevier coals; Slide 4c No. 34, Weir-Pittsburg Coal; × 59.

FIG. 4. Unidentified wood fragment; Slide 4a No. 26, Weir-Pittsburg Coal; × 59.

FIG. 5. Same; Slide 19a No. 2, Bevier Coal; × 59.

FIG. 6. Same; Slide 4a No. 26, Weir-Pittsburg Coal; × 59.

FIG. 7. *Lepidodendron?* tracheids; Slide 7c No. 25, Weir-Pittsburg Coal; × 59.

FIG. 8. Unidentified wood fragment; Slide 7a No. 16, Weir-Pittsburg Coal; × 59.

FIG. 9. Same; Slide 4c No. 26, Weir-Pittsburg Coal; × 59.

PLATE 3

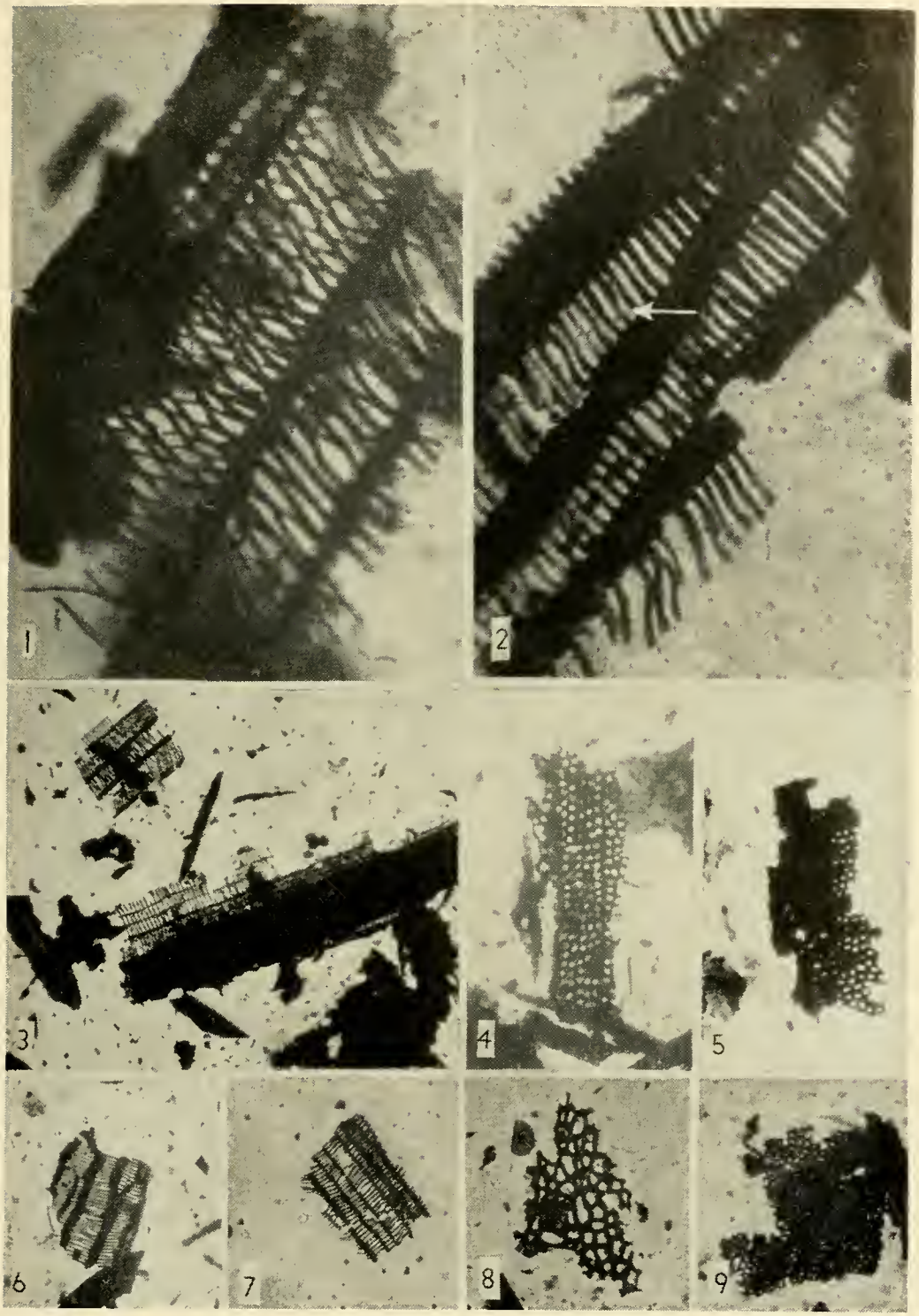


PLATE 4

AUTHOR'S NOTE: In all cases in the following plate explanations, the word, cell, refers to the imprint or shape of the plant cells which are preserved in the cuticle.

FIG. 1. Tracheid of *Medullosa*?; rare in all coals studied in this report; Slide 7a No. 16, Weir-Pittsburg Coal; × 271.

FIG. 2. Same; Slide 19b No. 8, Bevier Coal; × 271.

FIG. 3. Same; Slide 19a No. 2, Bevier Coal; × 271.

FIG. 4. Unidentified tracheids that may be Lycopodian; Slide 19a No. 2, Bevier Coal; × 271.

FIG. 5. Cortical strands of Lycopodian affinities; Slide 7c No. 22, Weir-Pittsburg Coal; × 271.

FIG. 6. Cuticle; diamond-shaped cells averaging 15-20 microns on a side; may be caused by one portion of cuticle with rectangular cells being folded over another portion of the same type of cuticle in a diagonal manner; Slide 19a No. 2, Bevier Coal; × 59.

FIG. 7. Same; slide 6a No. 40, Weir-Pittsburg Coal; × 271.

FIG. 8. Cuticle with polygonal-shaped cells; cell walls are rather thick; may be from a megaspore similar to figure 1, plate 24; Slide 19a No. 2, Bevier Coal; × 271.

FIG. 9. Cuticle with wavy, elongated cells averaging approximately 110-120 microns in length by 10-20 microns in width; found only in the Wier-Pittsburg, rare; Slide 6a No. 40, Weir-Pittsburg Coal; × 59.

FIG. 10. *Cordaites* cuticle; dense, narrow rows of cells; Slide 19a No. 4, Bevier Coal; × 59.

FIG. 11. Similar to Wilson and Hoffmeister's (1956) Cuticle type B; film-like and apparently structureless; network of pits is not as apparent as in figure 1, plate 6; approximately one micron thick; usually much folding is present; very similar to figure 2 on plate 6, but no perforations are present in this specimen; sparcely distributed throughout the Bevier and Weir-Pittsburg samples; Slide 19c No. 11, Bevier Coal; × 59.

FIG. 12. Similar to Winslow's (1959) Plate 16, figure 4; resembles cellular pattern from lower epidermis of *Cordaites* leaf; both lateral and terminal cells are shared by each stomate; stomata occur in rows of approximately 6; lateral cells are broader and shorter than ordinary epidermal cells and are approximately 50-60 microns in length by 25-33 microns in width; terminal cells are nearly always round, but sometimes oval and average 10-18 microns in diameter; ordinary epidermal cells are approximately 75-85 microns in length by 15-25 microns in width and are distinctly rectangular; Slide 4a No. 26, Weir-Pittsburg Coal; × 59.

FIG. 13. *Cordaites* cuticle similar to figure 12; Slide 6b No. 42, Weir-Pittsburg Coal; × 59.

FIG. 14. *Cordaites* cuticle; see figure 1, plate 23 for description; Slide 4a No. 26 Weir-Pittsburg Coal; × 59.

PLATE 4

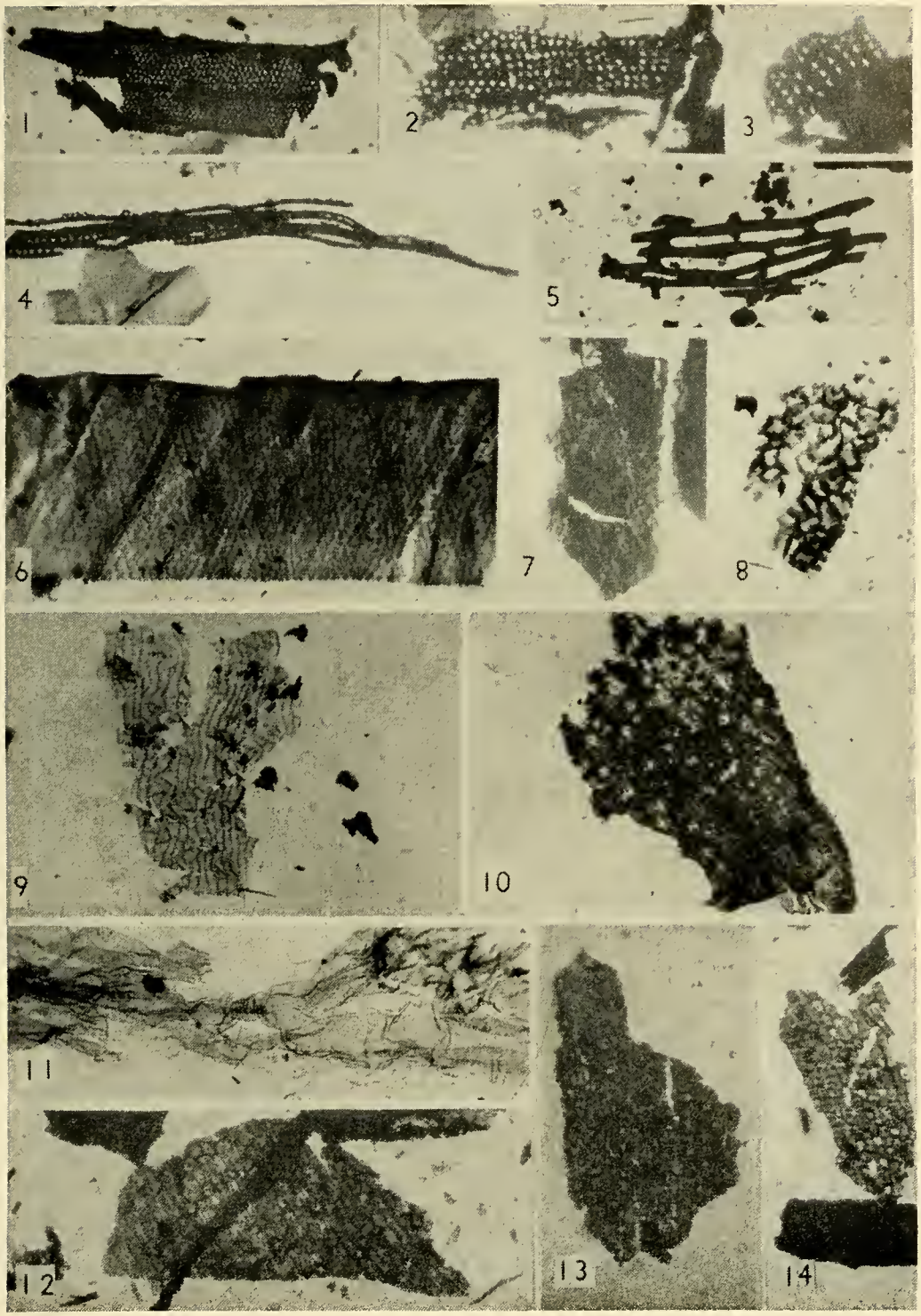


PLATE 5

FIG. 1. Cuticle with perforations 45-50 microns in diameter surrounded by polygonal-shaped cells averaging approximately 25-30 microns on a side; Slide 4a No. 26, Weir-Pittsburg Coal; × 59.

FIG. 2. Similar to Winslow's (1959) plate 16, figure 5; cuticle with openings averaging approximately 30-34 microns in diameter and which are surrounded by polygonal-shaped cells; these openings may be stomatal in nature; rare; Slide 19a No. 4, Bevier Coal; × 59.

FIG. 3. Similar to Winslow's (1959) plate 16, figure 7; cuticle has dome cells and cuticular crests and resembles some of Bartlett's (1929) plates; probable affinity is *Lepidodendron*; rare in all coals studied in this report; Slide 7c No. 25, Weir-Pittsburg Coal; × 59.

FIG. 4. Cuticle with conspicuous perforations approximately 28-33 microns in diameter, surrounded by polygonal-shaped cells averaging 25-30 microns on a side; may be associated with such genera as *Dolerotheca,* male fructification of Whittleseyinae; rare; for more complete description see figure 1, plate 22; Slide 19a No. 2, Bevier Coal; × 271.

FIG. 5. Cuticle with elongated cells associated with long strings of variously-sized perforations; cells are approximately 95-100 microns long by 25-30 microns wide; Slide 6a No. 37, Weir-Pittsburg Coal; × 271.

FIG. 6. Same; Slide 19c No. 11, Bevier Coal; × 59.

FIG. 7. Same; Slide 19c No. 11, Bevier Coal; × 59.

PLATE 5

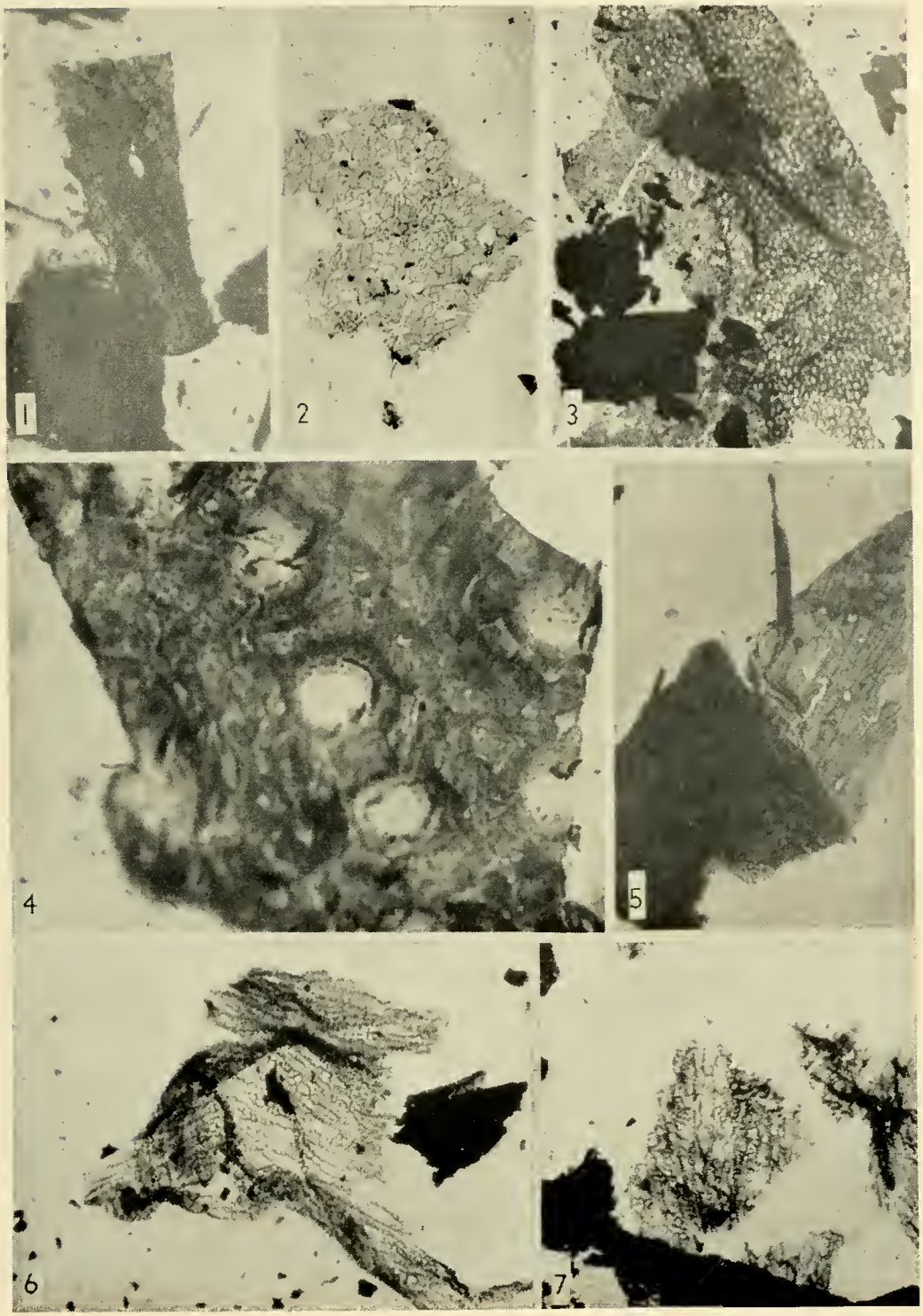


PLATE 6

FIG. 1. This material is probably not of plant origin; similar to Winslow's (1959) plate 16, figure 10; characterized by openings from 35-50 microns in diameter surrounded by closely-spaced depressions up to 12 microns in diameter; Winslow indicates that this may be membranes of animal origin; sparsely distributed throughout Weir-Pittsburg and Bevier Coals; Slide 19c No. 11, Bevier Coal; × 59.

FIG. 2. Similar to Wilson and Hoffmeister's (1956) Cuticle type B; structureless and less than one micron thick; folds are common; perforations are approximately 5-6 microns in diameter; Slide 19c No. 10, Bevier Coal; × 271.

FIG. 3. Similar to figure 2; perforations are about 10 microns in diameter surrounded by small depressions; Slide 19b No. 9, Bevier Coal; × 59.

FIG. 4. Irregularly-perforated material; perforations are about 20-25 microns in diameter; Slide 7a No. 15, Weir-Pittsburg Coal; × 59.

FIG. 5. Probably a small portion of the type of material pictured in figure 7; Slide 19a No. 5, Bevier Coal; × 59.

FIG. 6. Same; Slide 19a No. 4, Bevier Coal; × 59.

FIG. 7. Similar to Winslow's (1959) plate 16, figure 10; perforations are approximately 45-50 microns in diameter, surrounded by numerous small depressions approximately 6 microns in diameter; Slide 19b No. 9, Bevier Coal; × 59.

PLATE 6

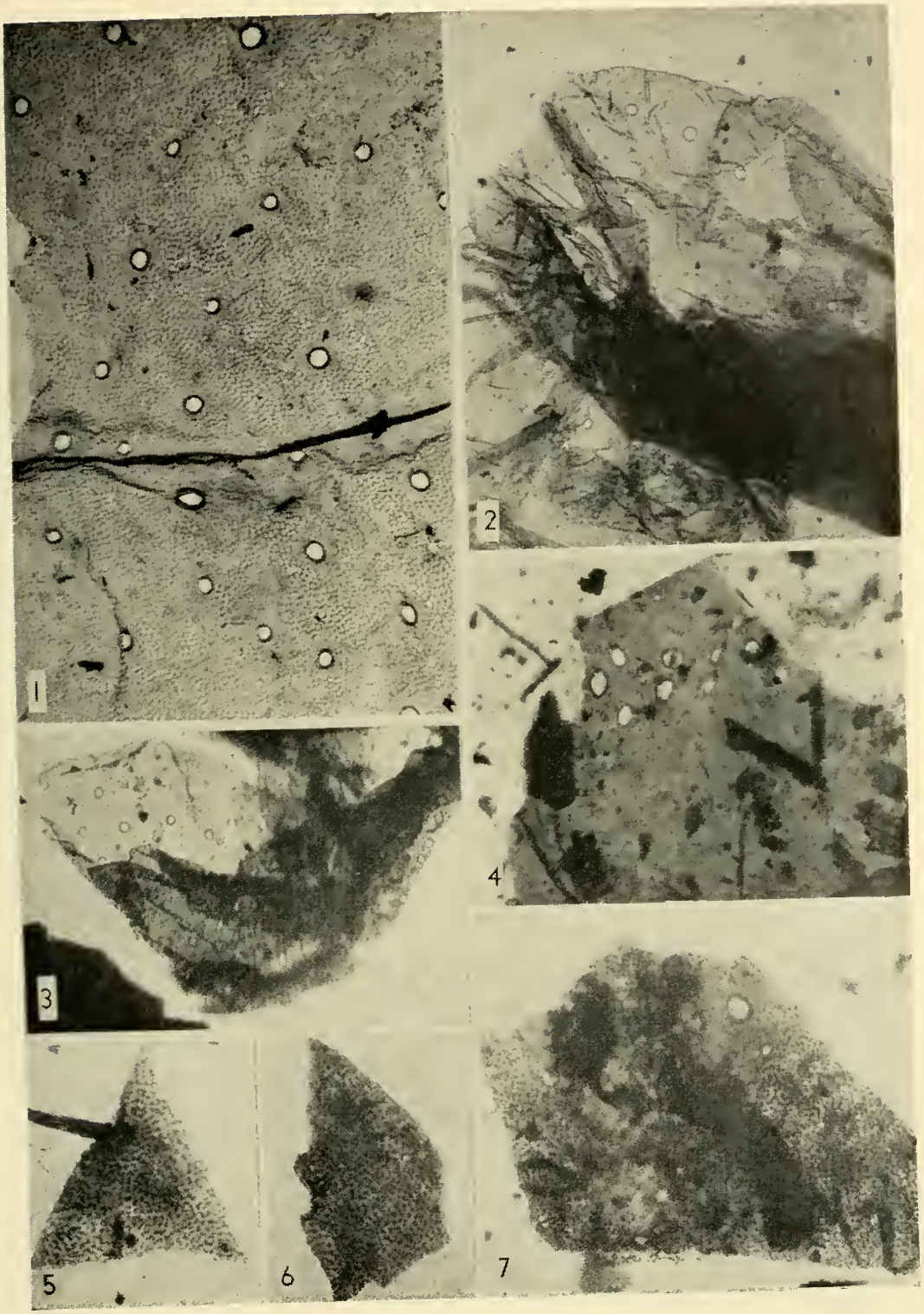


PLATE 7

FIG. 1. Leaf cuticle; cell walls are very prominent and approximately 2-3 microns thick; cell shapes are variable but mostly polygonal; Slide 19c No. 10, Bevier Coal; × 59.

FIG. 2. Similar to Wilson and Hoffmeister's (1956) Cuticle type D; stomatal structures may be present; hexagonal to polygonal cells; walls approximately one micron thick; average cell is approximately 45 microns on a side; Slide 19a No. 2, Bevier Coal; × 59.

FIG. 3. Cuticle with elongated cells, interfingering at ends; Slide 19a No. 2, Bevier Coal; × 59.

FIG. 4. Similar to Wilson and Hoffmeister's (1956) Cuticle type D; most of the cells are hexagonal or polygonal in shape, occasionally rectangular; walls approximately 1-2 microns thick; cells average approximately 45 microns on a side; most abundant form of cuticle in the Bevier Coal and is also plentiful in the Weir-Pittsburg; Slide 19a No. 2, Bevier Coal; × 59.

FIG. 5. Cuticle with extremely irregular shaped cells, with varied wall thicknesses; Slide 19a No. 2, Bevier Coal; × 59.

FIG. 6. Same as figure 4; Slide 19a No. 2, Bevier Coal; × 59.

FIG. 7. Upper surface of leaf?; cuticle with occasional perforations 3.5-4 microns in diameter; cells hexagonal to elongated and have fairly thin walls; note the interfingering effect; sparse distribution in both Weir-Pittsburg and Bevier Coals; Slide 19c No. 14, Bevier Coal; × 271.

PLATE 7

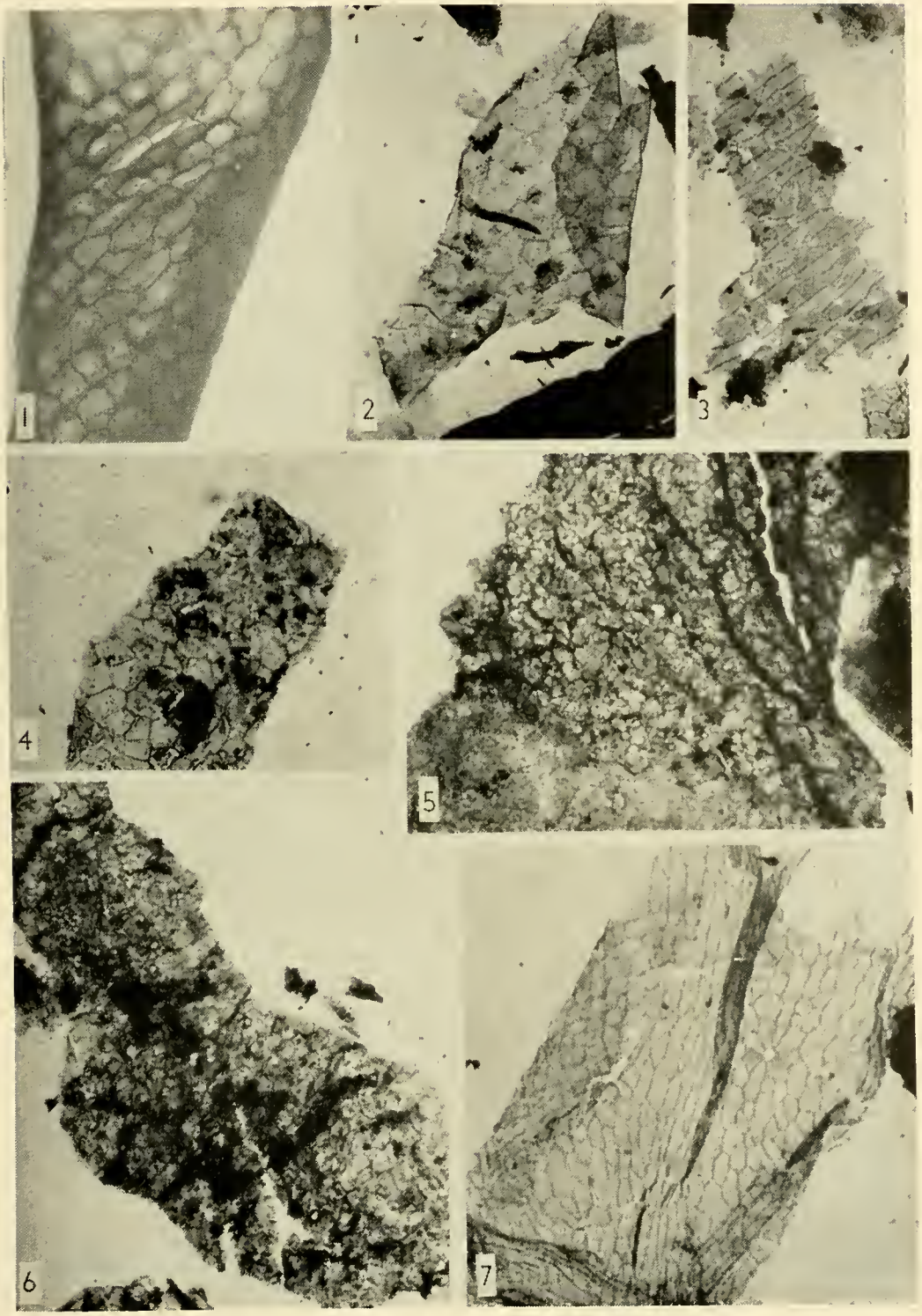
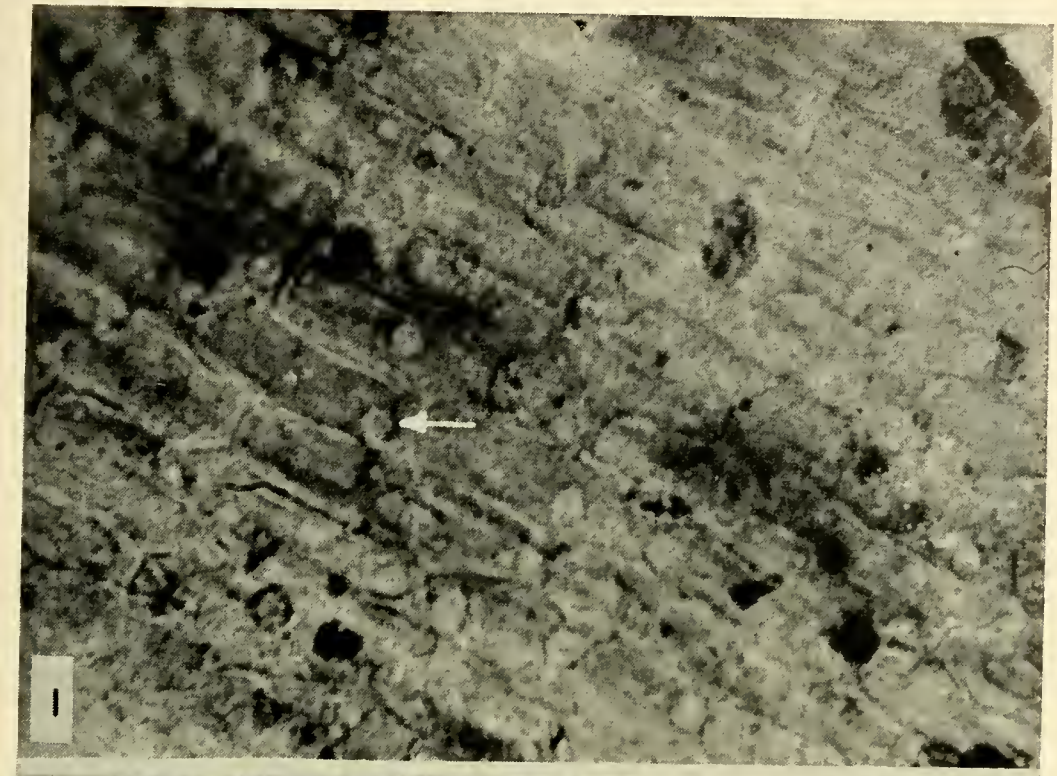


PLATE 8

FIG. 1. Cuticle with long thin cells associated with circular pits; pits (white arrow) are approximately 7 microns in diameter; cells average approximately 55 by 13 microns; rare, found only in Bevier Coal; Slide 19a No. 2, Bevier Coal; × 390.

FIG. 2. Cuticle with irregular polygonal-shaped cells; cells are thin-walled, less than 1 micron thick; cells average approximately 50 microns on a side; fairly common in all coals studied; Slide 19a No. 2, Bevier Coal; × 390.

PLATE 8



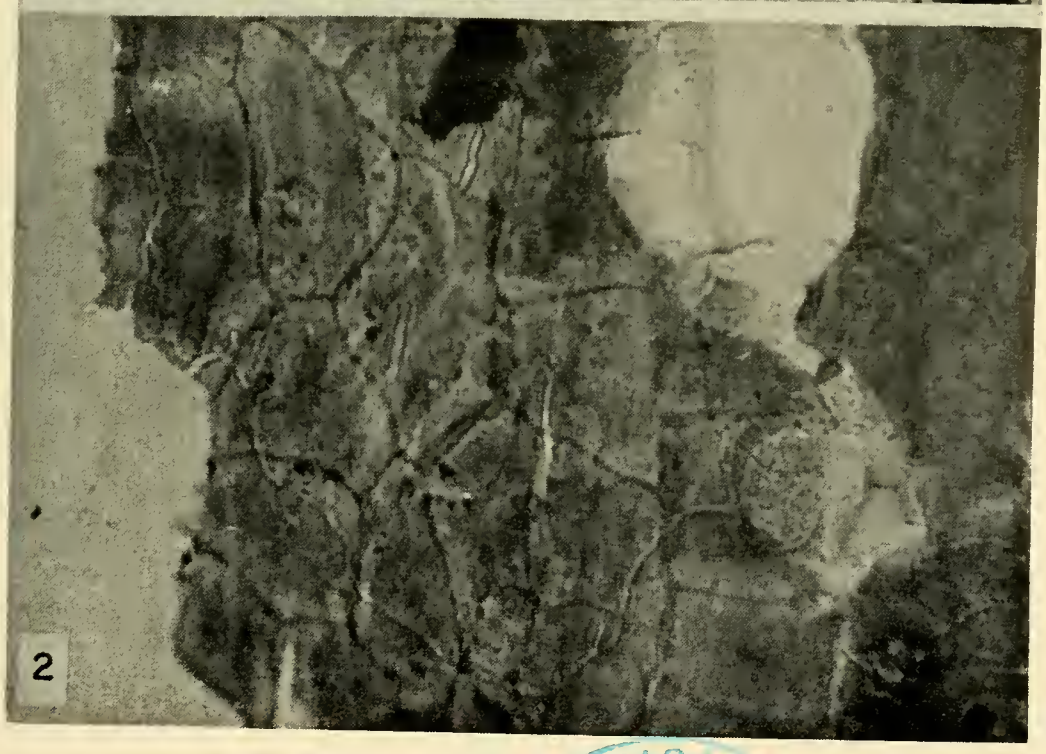


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PLATE 9

FIG. 1. Cordaitean cuticle; cells are oblong, with lengths averaging about 45-95 microns in length by 15-35 microns in width; Slide 19a No. 2; Bevier Coal; × 59.

FIG. 2. Similar to Wilson and Hoffmeister's (1956) Cuticle type A; cells are mostly rectangular; Slide 19a No. 2; Bevier Coal; × 59.

FIG. 3. Similar to Wilson and Hoffmeister's (1956) Cuticle type A; probably Cordaitean; cells are long and rectangular and average from 12 to 24 microns in width to 40-75 microns in length; cell walls are approximately 1.5-2 microns thick; one of the most abundant types of cuticle found in the Weir-Pittsburg Coal; Slide 19a No. 4, Bevier Coal; × 59.

FIG. 4. Similar to figure 3 but cells are much smaller and more narrow; walls are fairly thick; almost identical with specimens known to be *Cordaites;* Slide 6b No. 47, Weir-Pittsburg Coal; × 59.

FIG. 5. Similar to figure 3; Cordaitean; Slide 6b No. 44; Weir-Pittsburg Coal; × 271.

FIG. 6. Cuticle with cells extremely long and narrow; some are as long as 250 microns and longer; widths average about 20 microns; cell walls are very thin; Slide 19c No. 10; Bevier Coal; × 59.

FIG. 7. Cuticle similar to figures 5 and 3; Slide 6a No. 38; Weir-Pittsburg Coal; × 271.

PLATE 9

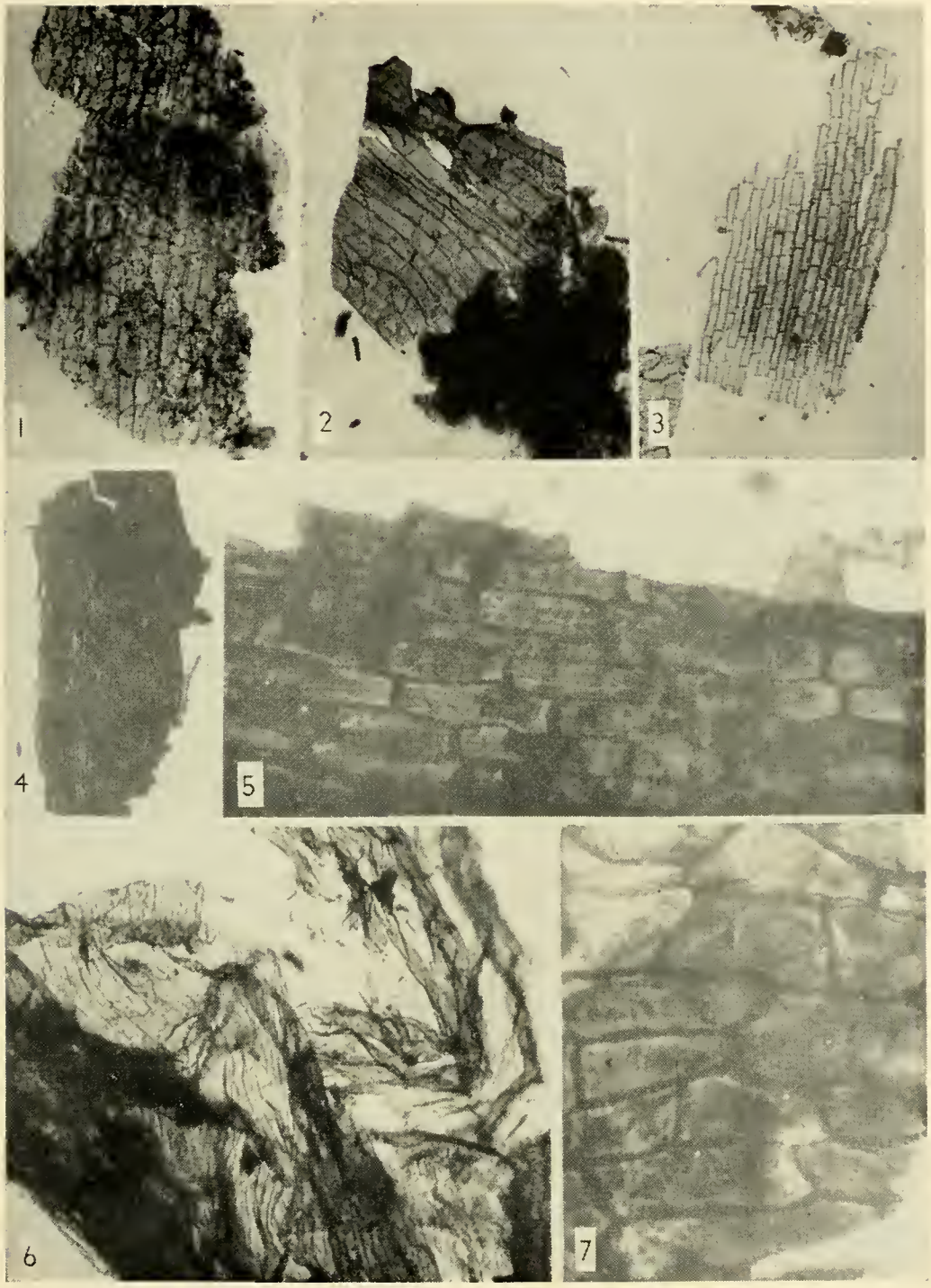


PLATE 10

FIG. 1. Cuticle with cells that are typically square- to slightly rectangular-shaped; cell walls are as much as 7 microns thick; cells average approximately 35 by 45 microns; Slide 19a No. 2, Bevier Coal; × 59.

FIG. 2. Portion of figure 1 enclosed in black lines; × 271.

FIG. 3. Compares favorably with Wilson and Hoffmeister's (1956) Cuticle type D; cells are polygonal- to squared-shaped and average approximately 50 by 35 microns; cell walls are approximately 2 microns thick; Slide 19a No. 2, Bevier Coal; × 59.

FIG. 4. Portion of figure 3 enclosed in black lines: × 271.

FIG. 5. Cuticle with thick-walled polygonal- to hexagonal-shaped cells; walls are apparently approximately 5-6 microns thick; the average cell side is approximately 15 microns; believed to be closely related to cuticle of *Lepidocarpon* megaspores, see plate 24, figure 1; fairly common in all coals studied; Slide 19c No. 14, Bevier Coal; × 59.

FIG. 6. Cuticle with cell walls that are very irregular in size and shape and in wall thickness; compares favorably with larger cuticle fragments taken from *Cordaites* leaf fragments; Slide 4c No. 34, Weir-Pittsburg Coal; × 59.

PLATE 10

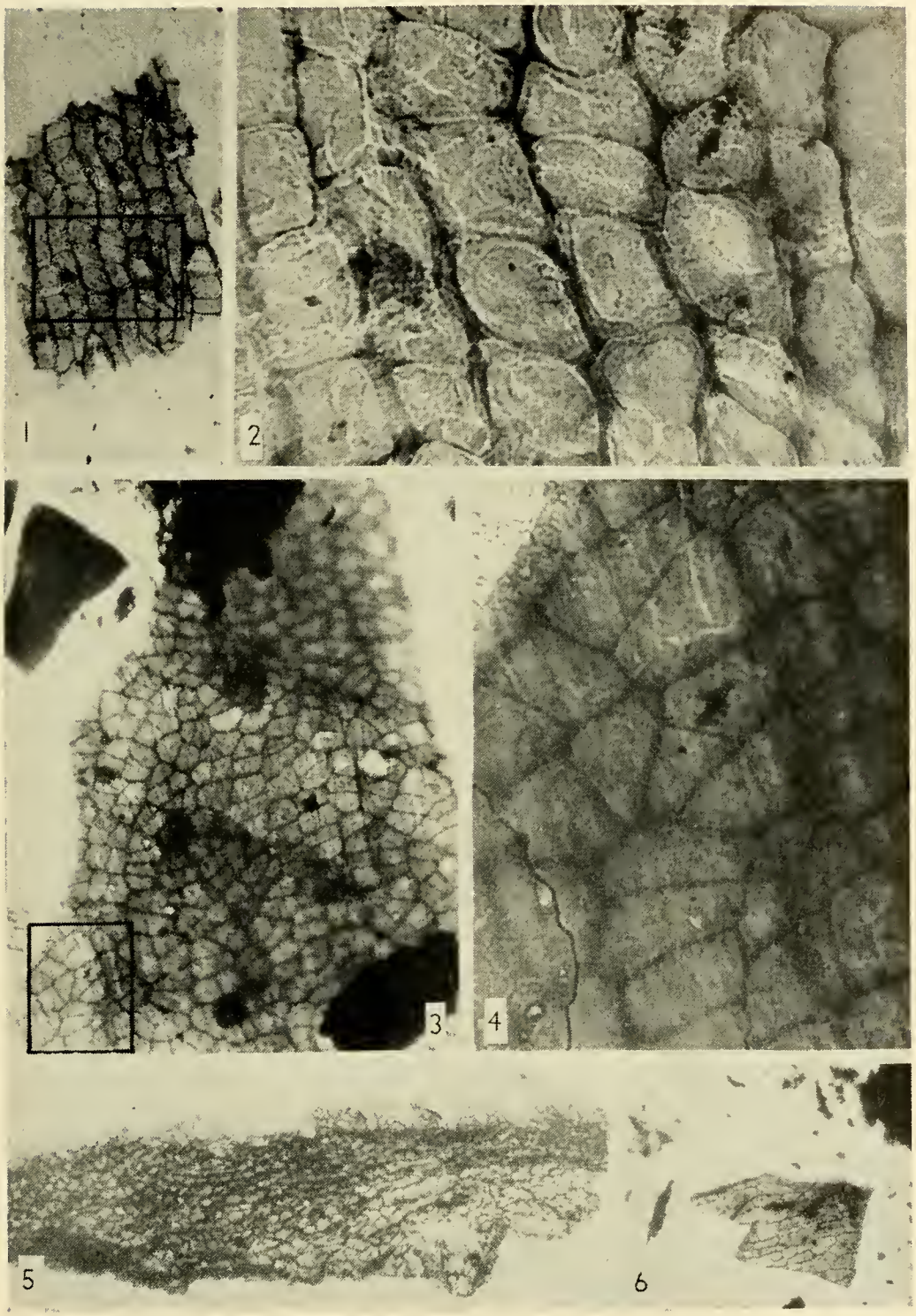


PLATE 11

FIG. 1. Cuticle of unknown affinities apparently without structures of any kind except thick-walled perforations averaging 10-18 microns in diameter; Slide 51, Bottom of Lower Williamsburg Coal; × 85.

FIG. 2. Cordaitean tracheids?; characterized by alternating rows of elliptical openings, 1.5-2 microns in diameter; common in Blue Mound and Lower Williamsburg Coals; Slide 51, Bottom of Lower Williamsburg Coal; × 625.

FIG. 3. Unidentified wood fragment (Lycopodian?); openings average 13 microns in length and approximately 5 microns in width; Slide 57, Bottom of Lower Williamsburg Coal; × 390.

FIG. 4. *Cordaites* secondary tracheid with multiseriate bordered pits; openings average about 4 microns in length and approximately one micron in width; these tracheids usually average about 6-8 pits in width; rare to common in Lower Williamsburg Coal; Slide 54, Bottom of Lower Williamsburg Coal; × 625.

FIG. 5. *Cordaites* tracheids; common; Slide 56, Bottom of Lower Williamsburg Coal; × 390.

FIG. 6. Unidentified fusainized fragment with holes averaging approximately 2.5-4 microns in diameter; fairly common in Middle of Lower Williamsburg Coal; Slide 62, Middle of Lower Williamsburg Coal; × 390.

PLATE 11

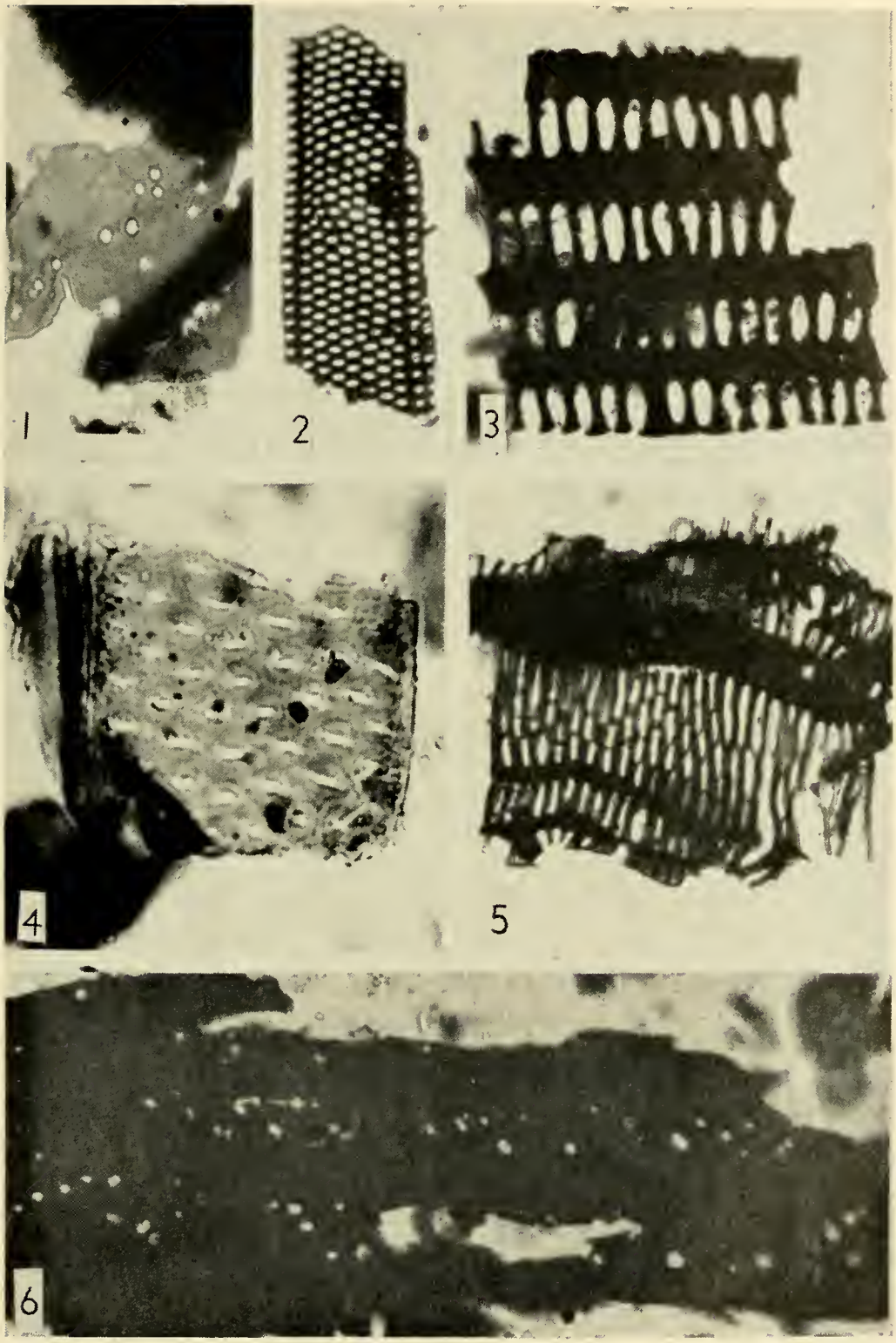


PLATE 12

FIG. 1. Unidentified fragment with variable circular openings ranging from 35 to 2 microns in diameter; common to rare in the Lower Williamsburg and Blue Mound Coals; Slide 94, Blue Mound Coal; × 390.

FIG. 2. Unidentified wood fragment with variable circular openings ranging from approximately 5-10 microns; common to rare in Blue Mound and Lower Williamsburg Coals; Slide 56, Bottom of Lower Williamsbur Coal × 390.

PLATE 12

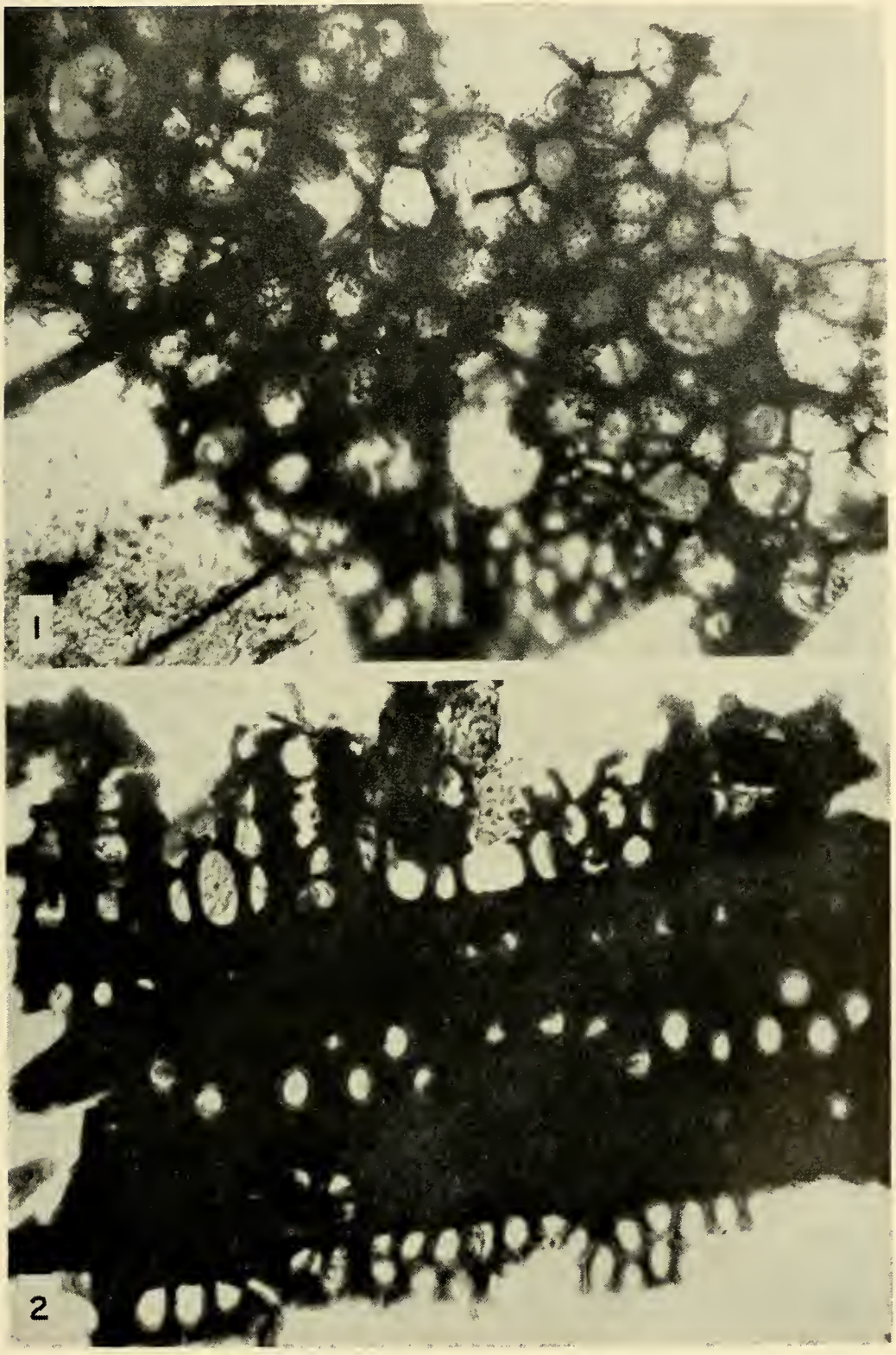


PLATE 13

FIG. 1. Tracheid from transition zone between primary and secondary xylem of *Cordaites*?; this fragment probably occurred between the protoxylem and scalariform tracheids of a Cordaitean-type plant; fairly common in the Weir-Pittsburg, Lower Williamsburg and Blue Mound Coals; Slide 63, Middle of Lower Williamsburg Coal; × 526.

FIG. 2. Leaf cuticle of *Cordaites*; this is the most abundant type present in the Lower Williamsburg and Blue Mound Coals; occasional pits and openings with a diameter of 11-12 microns; cell walls 3-6 microns thick; cells average about 80 by 23 microns and are wedge-shaped at the ends; Slide 97, Blue Mound Coal; × 85.

FIG. 3. Sac-shaped mass of square cells averaging about 40-50 microns on a side; rare; Slide 52, Bottom of Lower Williamsburg Coal; × 85.

FIG. 4. Cuticle characterized by square-shaped cells approximately 12 microns on a side; cell walls are thick and average 2-4 microns in thickness; Slide 75, Bottom of Lower Williamsburg Coal; × 390.

PLATE 13

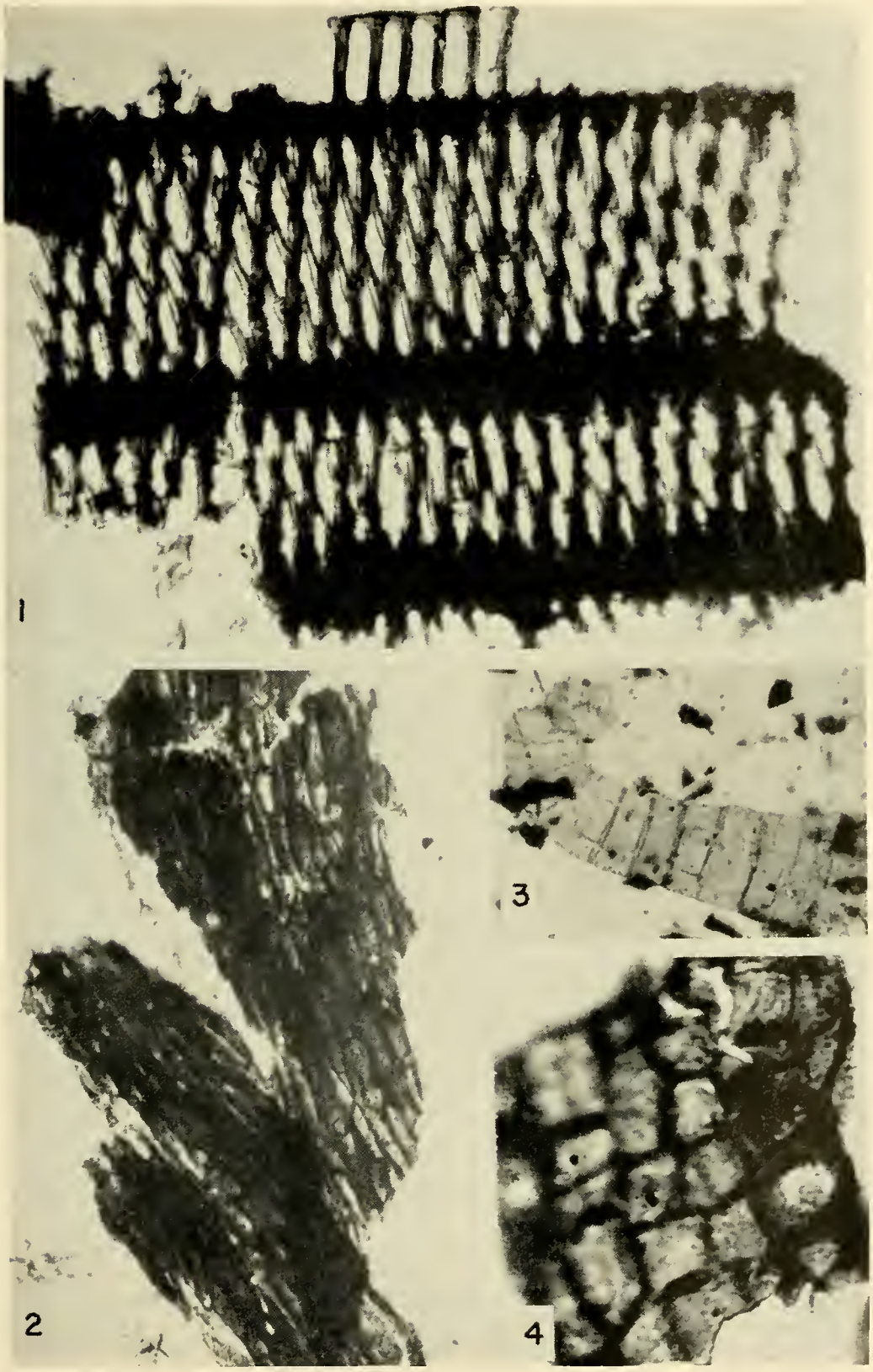


PLATE 14

FIG. 1. Cuticle with irregular elongated polygonal-shaped cells approximately 100 microns in length; cell walls 2.5-3 microns thick; abundant in Blue Mound and Lower Williamsburg Coals; Slide 97, Blue Mound Coal; × 57.

FIG. 2. Enlarged area framed in white in figure 1; × 260.

FIG. 3. Cuticle with elongated irregular-shaped cells averaging approximately 60 microns in length and 20 microns in width; fairly common in both Blue Mound and Lower Williamsburg Coals; Slide 97, Blue Mound Coal; × 260.

FIG. 4. Enlarged portion of figure 3.

PLATE 14

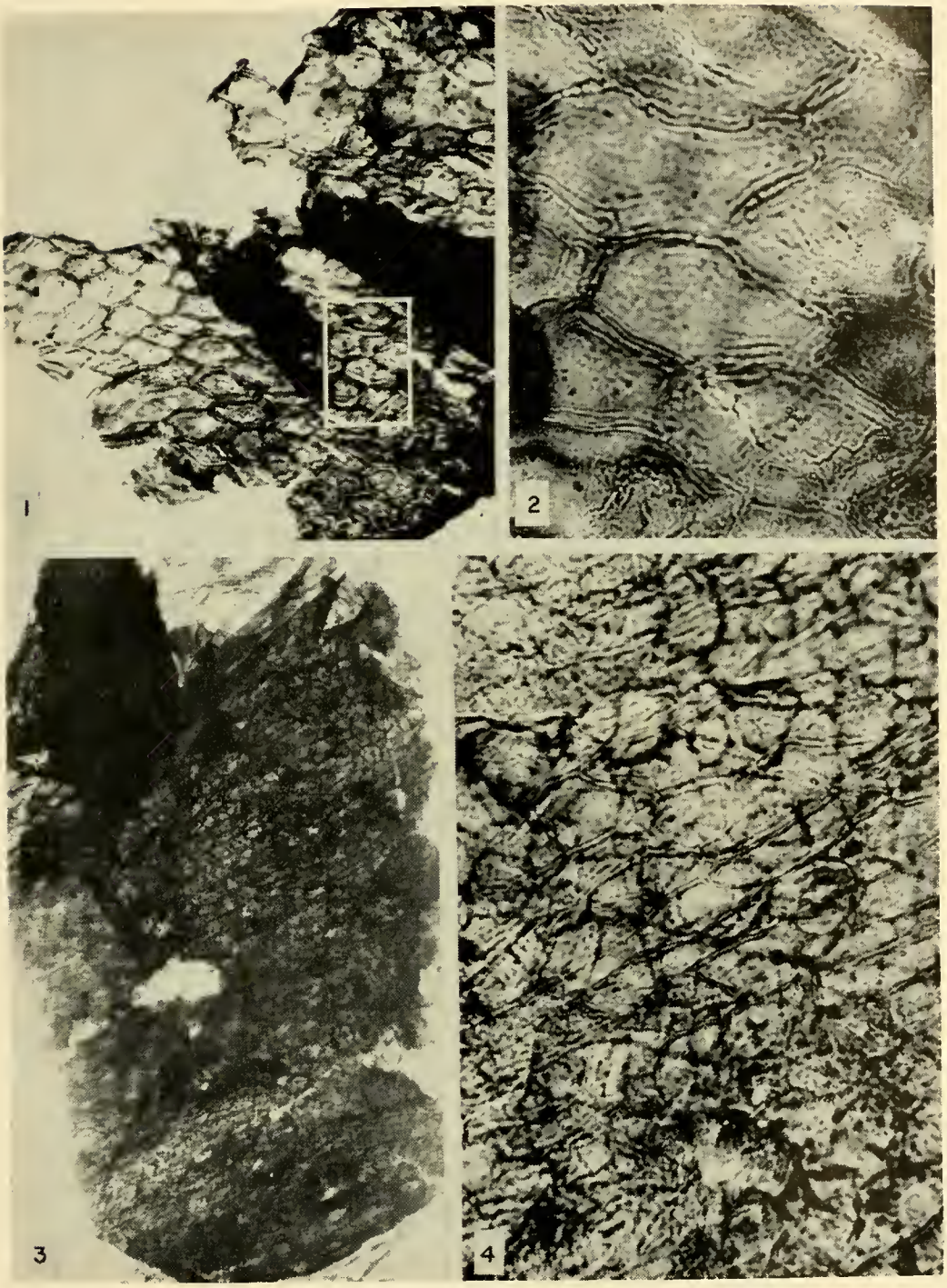


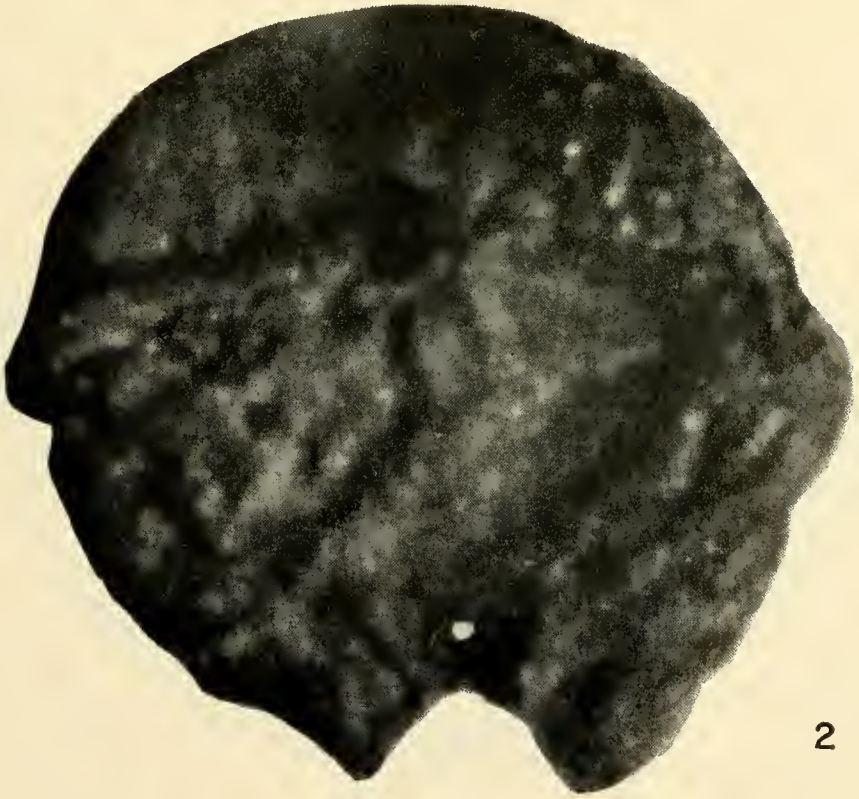
PLATE 15

FIG. 1. *Triletes* sp.; note the prominent undulating rays and the coarse rugose network covering the surface; conspicuous "wrinkles" are approximately 50 microns wide and form sharp to rounded ridges; diameter is 2000 microns; rare in the Blue Mound and Lower Williamsburg Coals; this specimen was taken from the Blue Mound Coal; × 42; reflected light.

FIG. 2. Opposite side of same specimen.

PLATE 15

1



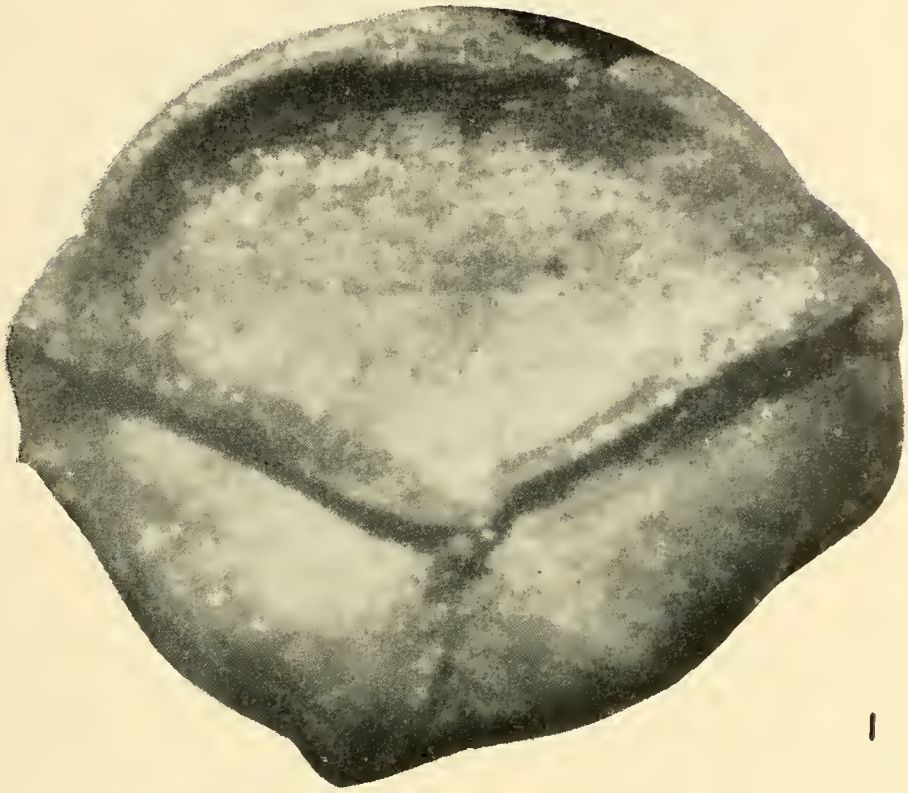
2

PLATE 16

FIG. 1. *Triletes* (sectio *Auriculati*) sp.; proximal view of proximo-distal compression with conspicuous darkened rays and darkened outer margin; rather smooth surface; ray ridges rather low in relief; diameter is 2100 microns; from Blue Mound Coal; × 42; reflected light.

FIG. 2. Distal view of same specimen.

PLATE 16



1

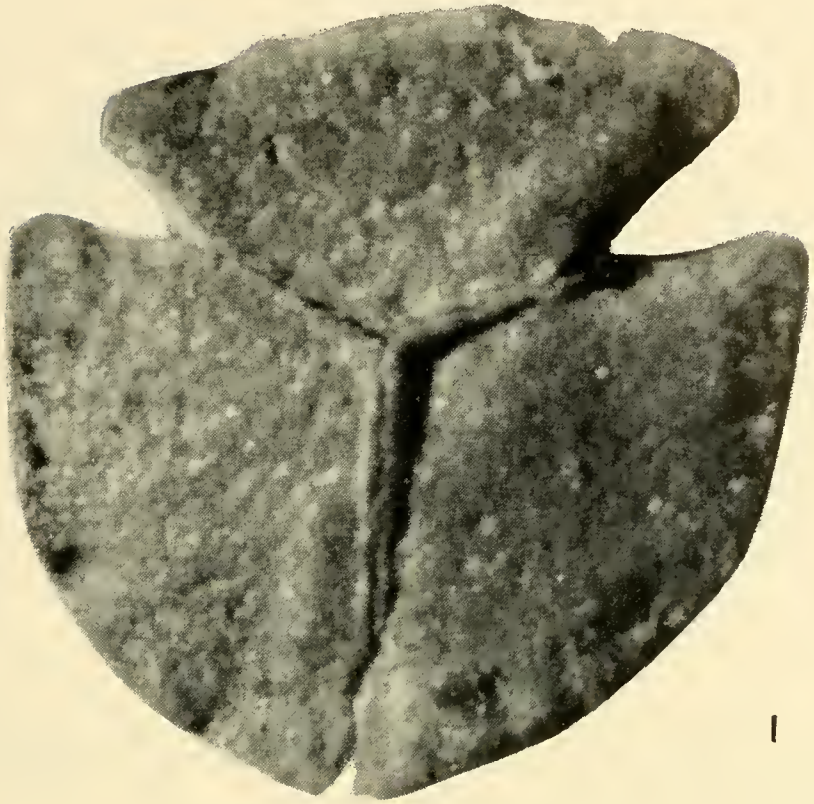
2

PLATE 17

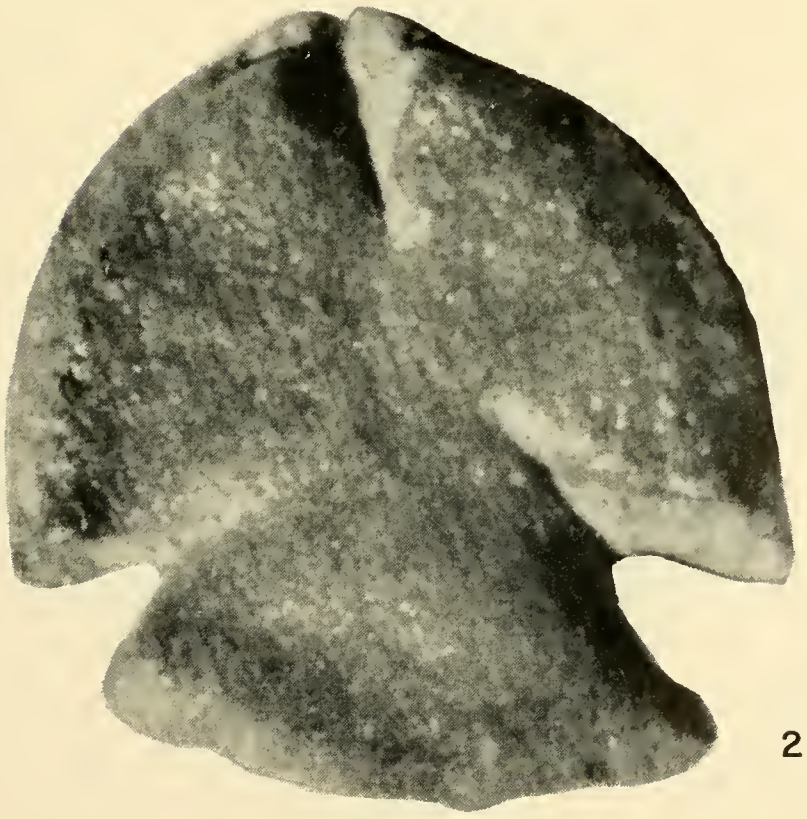
FIG. 1. *Triletes* sp.; proximal view of proximo-distal compression with conspicuous indentions along rays; conspicuous furrow along top of rays; rays decrease in relief toward the indented areas; rare, most frequent in top portion of Lower Williamsburg Coal; diameter 1900 microns; × 42; reflected light.

FIG. 2. Distal view of same specimen.

PLATE 17



1



2

PLATE 18

FIG. 1. *Triletes* (sectio *Auriculati*) sp.; proximal view of proximo-distal compression with wide darkened rays; Top of Lower Williamsburg Coal; diameter 1900 microns; × 42, reflected light.

FIG. 2. Distal view of same specimen.

PLATE 18

1.

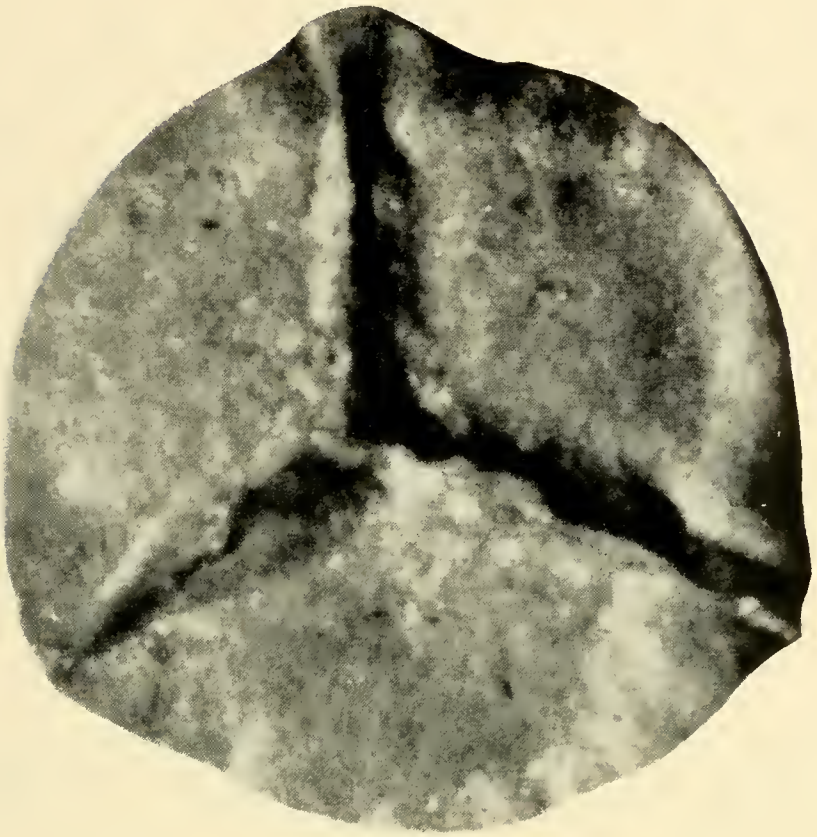
2

PLATE 19

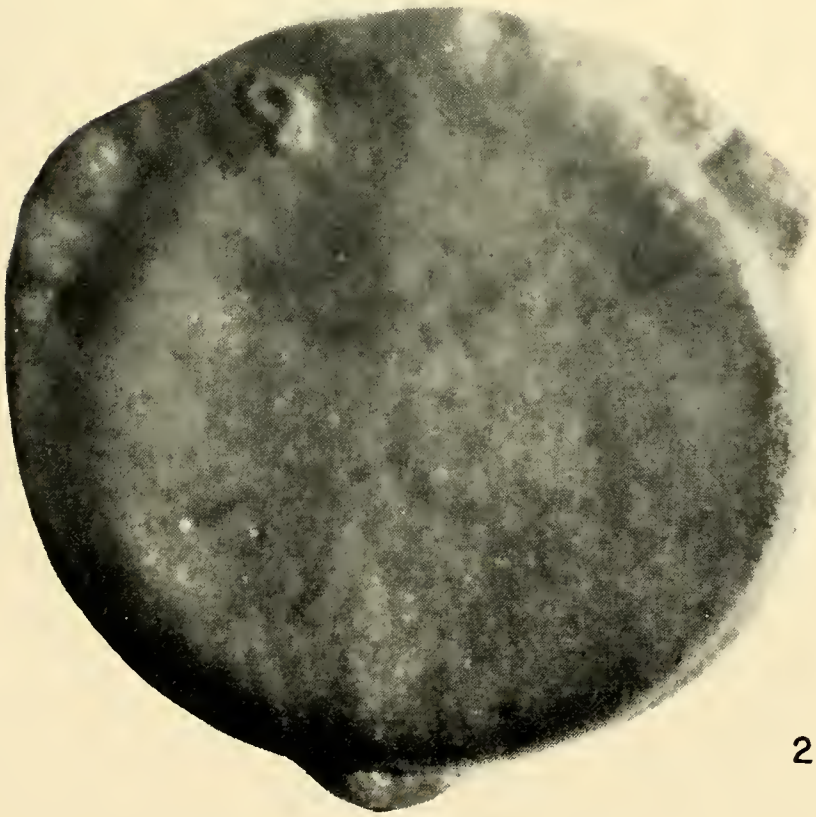
FIG. 1. *Triletes* (sectio *Auriculali*) sp.; proximo-distal compression with low slightly-undulating rays; rays darkened; surface relatively smooth; Bottom of Lower Williamsburg Coal; 1900 microns in diameter; × 42, reflected light.

FIG. 2. Distal view of same specimen.

PLATE 19



1



2

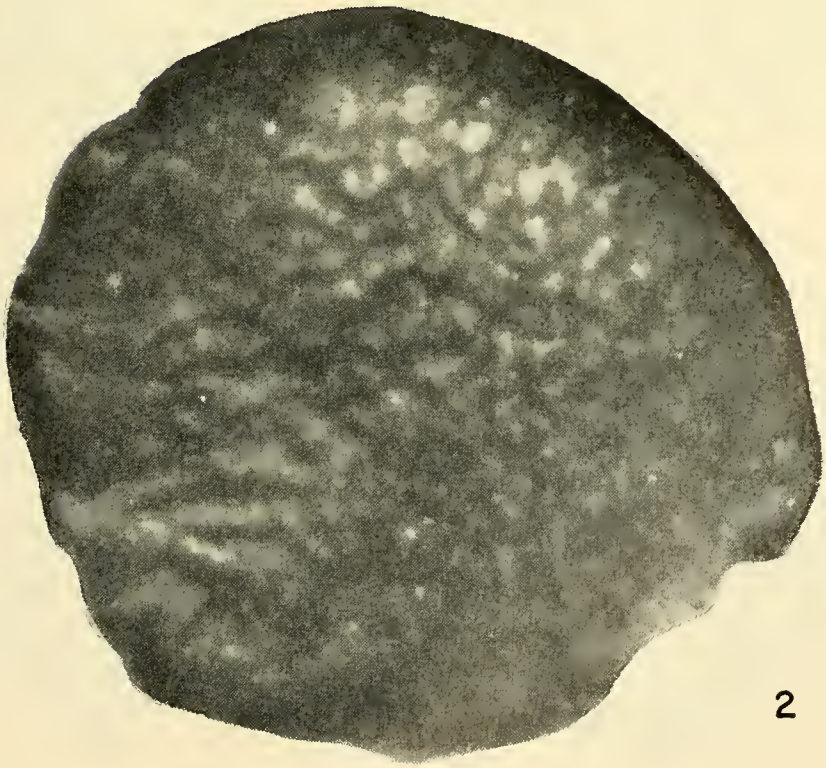
PLATE 20

FIG. 1. *Triletes* sp.; proximo-distal compression with low, darkened, slightly-undulating rays; Bottom of Lower Williamsburg Coal; 1825 microns in diameter; × 42; reflected light.

FIG. 2. Distal view of same specimen; note the network of "wrinkles."

PLATE 20

1



2

PLATE 21

FIG. 1. *Triletes* (sectio *Lagenicula*) *levis* (Zerndt) Schopf, Wilson and Bentall, 1944; lateral compression with blunt and conspicuous apical protuberance; may be associated with the organ genus *Sigillariostrobus* (see Dijkstra, 1958); common to abundant in Blue Mound and Lower Williamsburg Coals and is most abundant in the Middle part of Lower Williamsburg Coal; 1300 microns in total length; Middle of Lower Williamsburg Coal; × 42; reflected light.

FIG. 2. Opposite side of same specimen.

FIG. 3. *Triletes* (sectio *Lagenicula*) *levis* (Zerndt) Schopf, Wilson and Bentall, 1944; 1050 microns in total length; Middle of Lower Williamsburg Coal; × 42; reflected light.

FIG. 4. Opposite side of same specimen.

FIG. 5. *Triletes* (sectio *Auriculati*) sp.; outer margin well-defined; rays inconspicuous and poorly-developed; rays fade away at approximately ¾ the distance to the margin; Blue Mound Coal; approximately 1300 microns in diameter; × 42, reflected light.

FIG. 6. Opposite side of same specimen.

PLATE 21

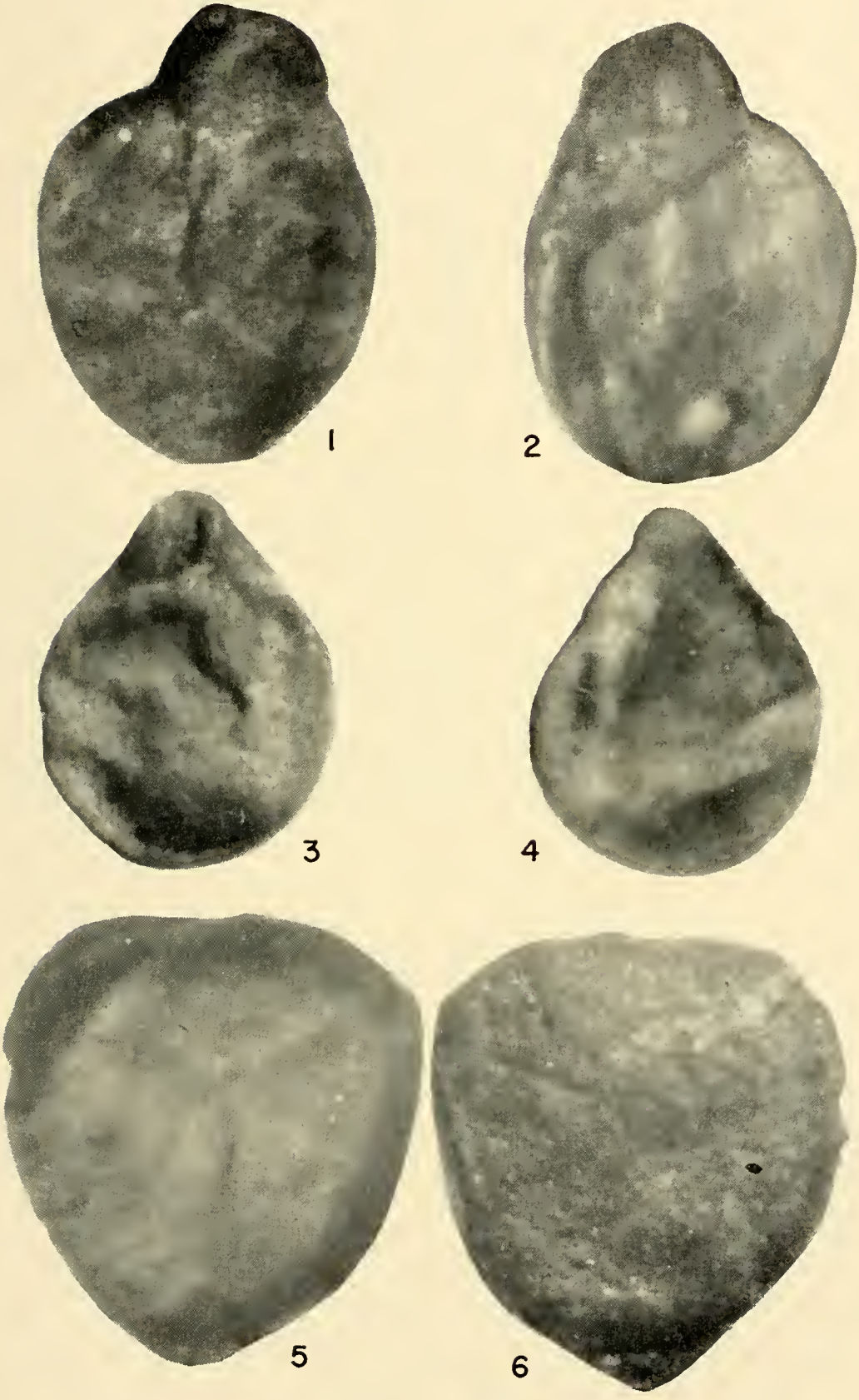
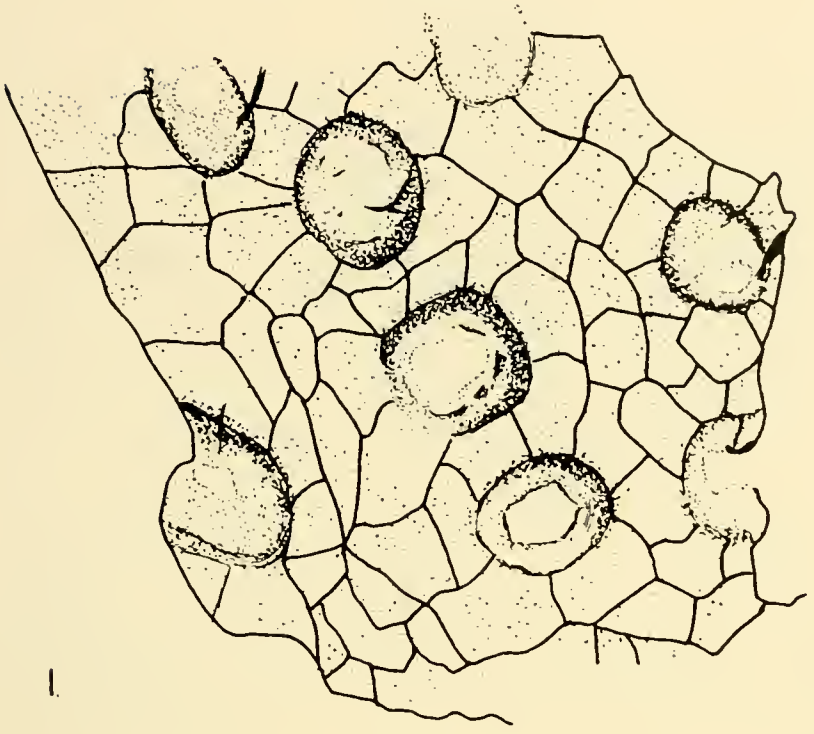


PLATE 22

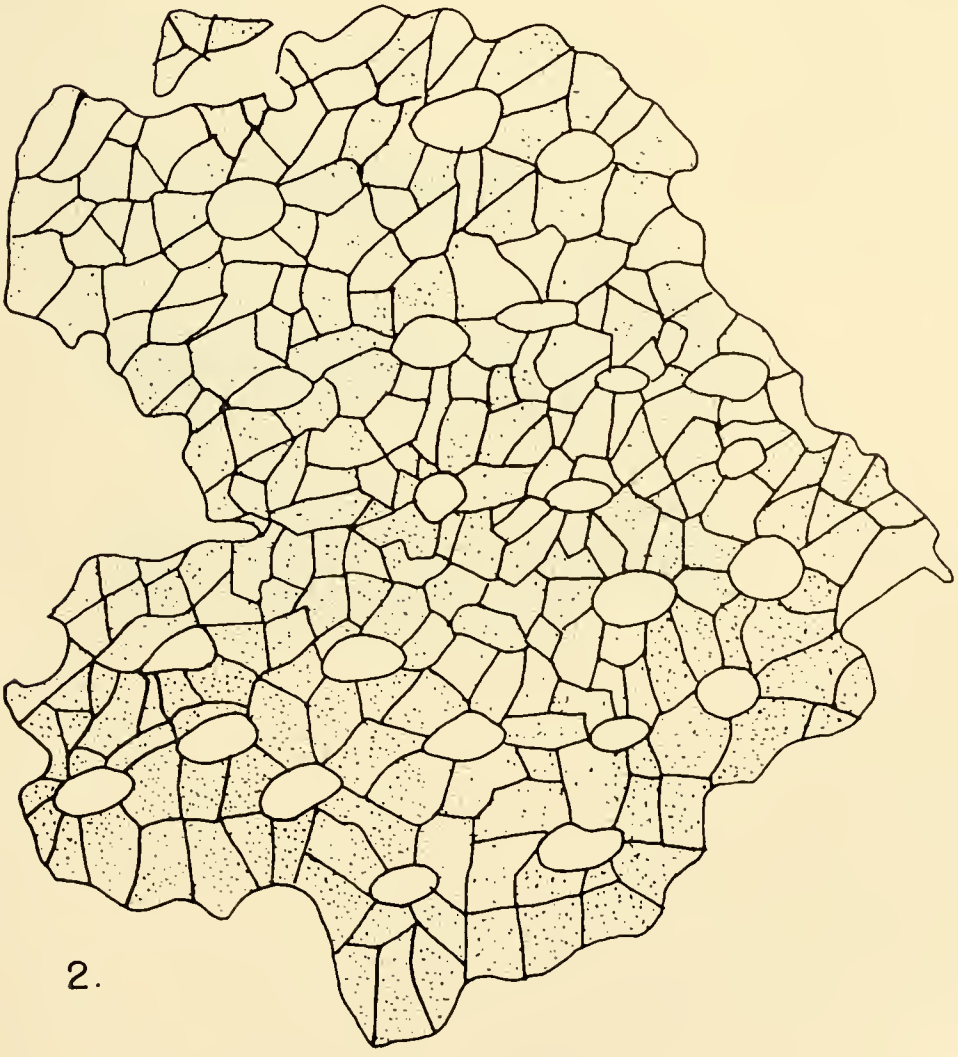
FIG. 1. Camera lucida drawing of figure 4, plate 5 of this report; thick cuticle with conspicuous perforations approximately 28-33 microns in diameter surrounded by polygonal-shaped cells; may be associated with *Dolerotheca* or related genera; closely resembles the cell pattern of the epidermis at the base of dorsal hairs; large perforations correspond to the position occupied by hairs; note heavy thickenings around perforations; rare, found only in the Bevier Coal; from slide 19a No. 2; × 312.

FIG. 2. Camera lucida drawing of cuticle shown in figure 2, plate 5; conspicuous openings averaging 35 microns in diameter; these openings might be stomatal in nature; rare; Slide 19a No. 4, Bevier Coal; × 172.

PLATE 22



1.



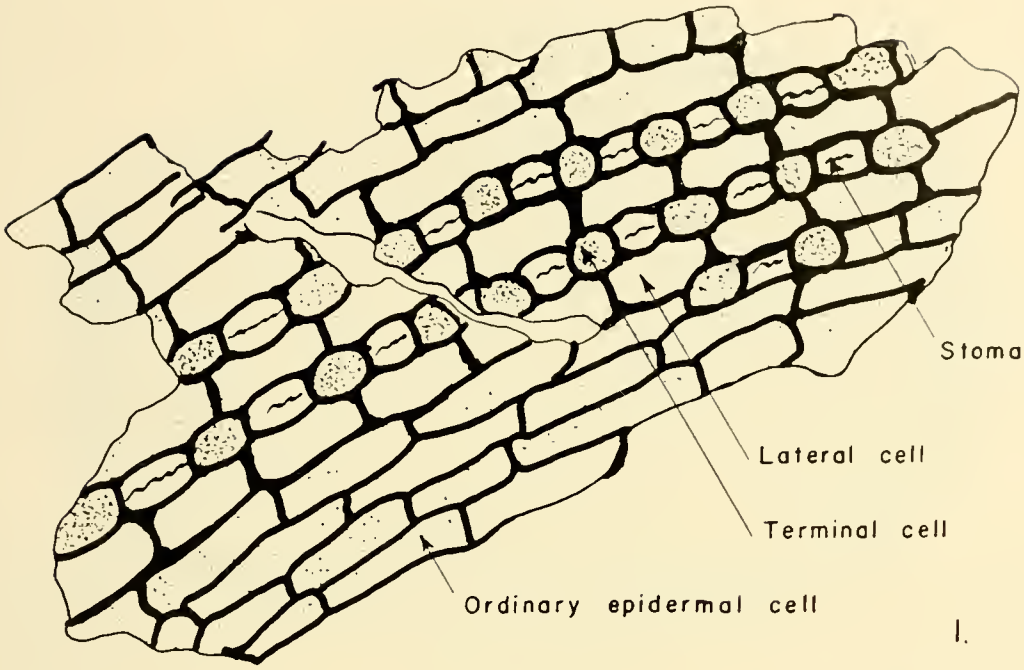
2.

PLATE 23

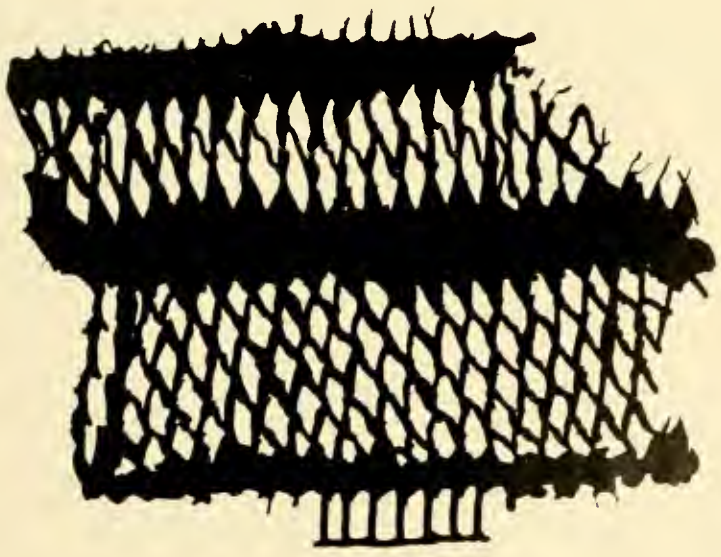
FIG. 1. Camera lucida drawing of figure 14, plate 3; note in both this drawing and the photograph on plate 3 how the terminal subsidiary cells are nearly always darker than the stomatal areas; resembles *Cordaites* lower epidermis cuticle of leaf; the stomata are closely crowded together and both the lateral and terminal cells are shared; the lateral cells are 45-55 microns in length by 15-25 microns in width; terminal cells are oval-shaped and average 20-30 microns in diameter; the lateral cells are broader and shorter than the ordinary epidermal cells; guard cells were not distinguishable; Slide 4a No. 26, Weir-Pittsburg Coal; × 236.5.

FIG. 2. Camera lucida drawing of transition zone between primary and secondary xylem of *Cordaites* tracheids; fairly common in the Weir-Pittsburg samples; × 434.7.

PLATE 23



1.



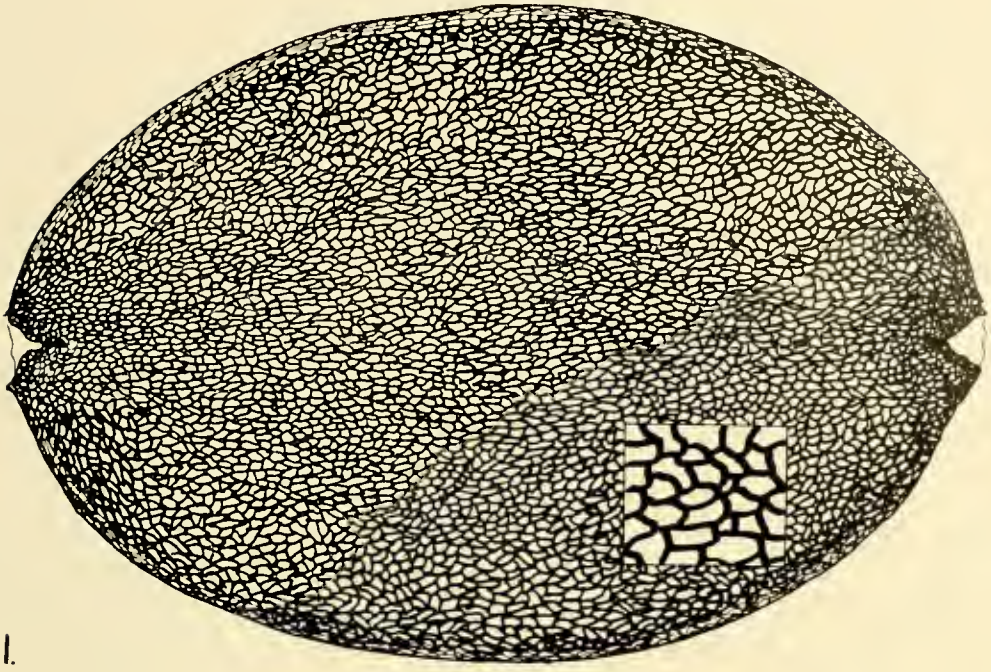
2.

PLATE 24

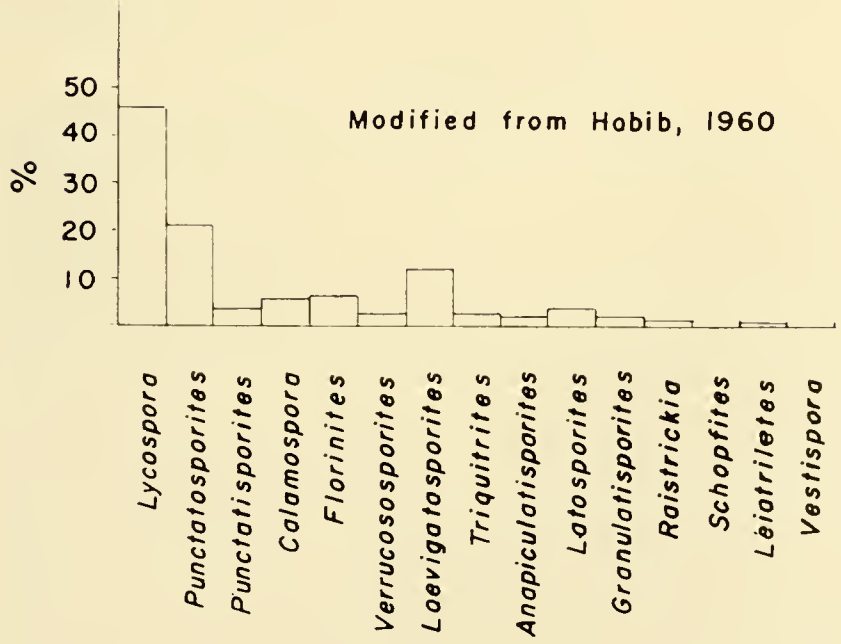
FIG. 1 *Lepidocarpon* megaspore taken from the Top of the Lower Williamsburg Coal; fairly common; this camera lucida drawing is of the largest specimen found during this study; usually these megaspores are only ⅔ to ½ this size, cuticle fragments scattered throughout the Lower Williamsburg, Bevier, Blue Mound and Weir-Pittsburg Coals bear a very close resemblance to this specimen; cell walls are irregular and thick; × 13.4, inset is × 53.5. The opening at the right end of the megaspore is a tear, not a morphological feature.

FIG. 2. Microspore histogram modified from Habib's (1960) thesis (see references); this histogram was prepared by using the same sample of Bevier Coal that was used for the investigation of cuticles and larger microflora in this report (from Bevier sample 19).

PLATE 24



1.


Modified from Hobib, 1960
%
50
40
30
20
10
Lycospora
Punctatosporites
Punctatisporites
Calamospora
Florinites
Verrucosisporites
Laevigatosporites
Triquitrites
Anapiculatisporites
Latosporites
Granulatisporites
Raistrickia
Schopfites
Leiotriletes
Vestispora

2.

PLATE 25

FIG. 1. Camera lucida drawing of cuticle fragment showing the relationship between polygonal-shaped cells and long, rectangular-shaped cells; cuticle of this type is not common but it shows at least a partial association of polygonal and rectangular cells; Slide 19b No. 7, Bevier Coal; × 200.

FIG. 2. Fragment of *Cordaianthus* sp. Grand 'Eury, *Cordaites* inflorescense; fragments of cuticle of this type are common in the Lower Williamsburg and Blue Mound Coals; cells are square to rectangular and sometimes hexagonal or polygonal, usually about 35 microns long in the specimen illustrated here; other specimens sometimes show somewhat smaller cells; cells have conspicuous wall thickenings; may correspond with Wilson and Hoffmeister's (1956) Cuticle type C; sex of the various strobili was undetermined; camera lucida drawing from Top of Lower Williamsburg Coal; × 36, inset × 108.

PLATE 25

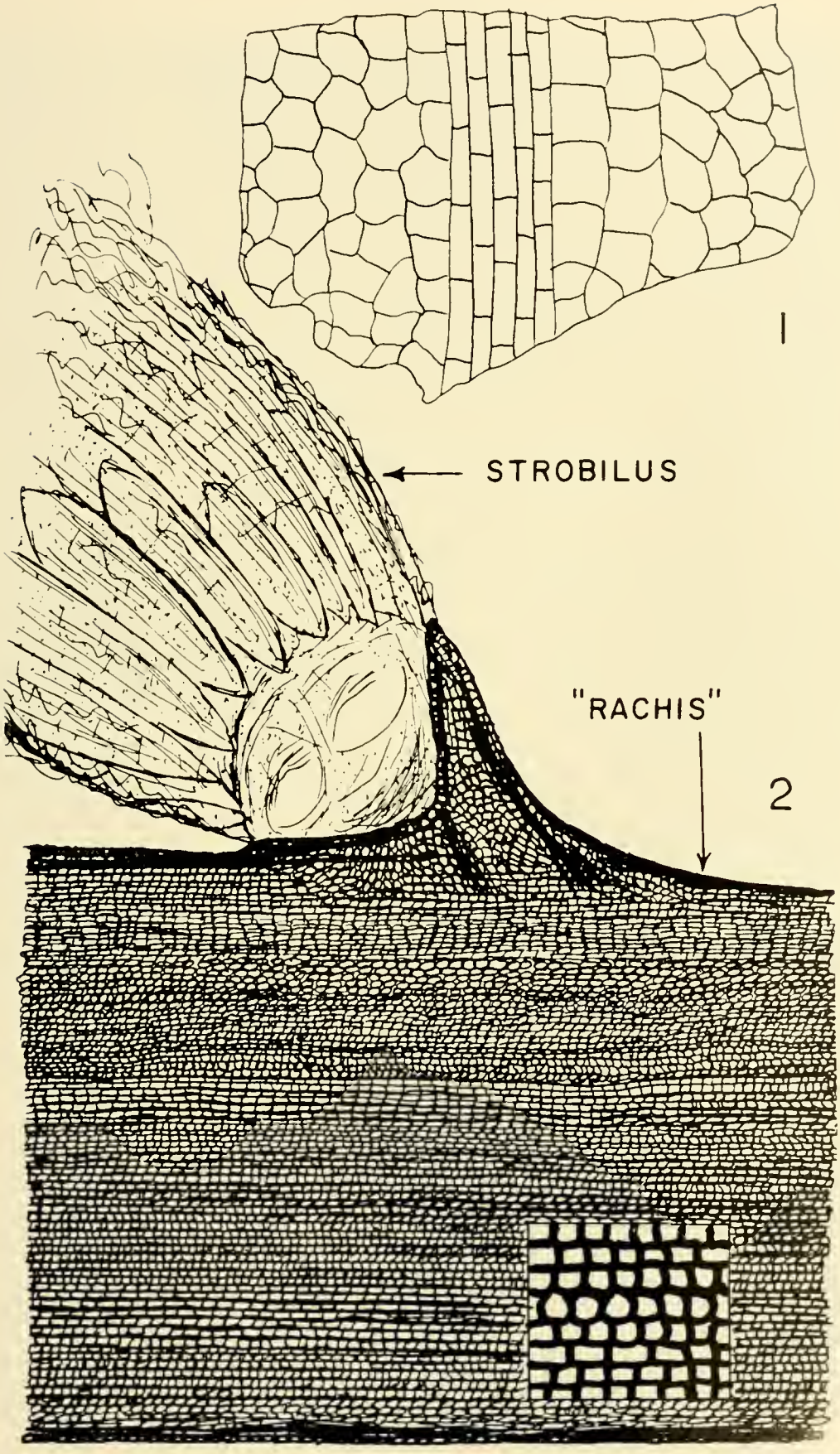


PLATE 26

Outcrop of Lower Williamsburg Coal in NW corner Sec. 13, Twp. 14 S., Range 18 E., Douglas County, Kansas, approximately 200 yards below Lone Star Lake Spillway. Exposed in this bank is about 14 feet of Lawrence Shale. Good compressions of *Neuropteris scheuchzeri* Hoffm., *Pecopteris, Annularia,* etc., may be found here in the Lawrence shale a few inches above the Lower Williamsburg Coal bed.

PLATE 26

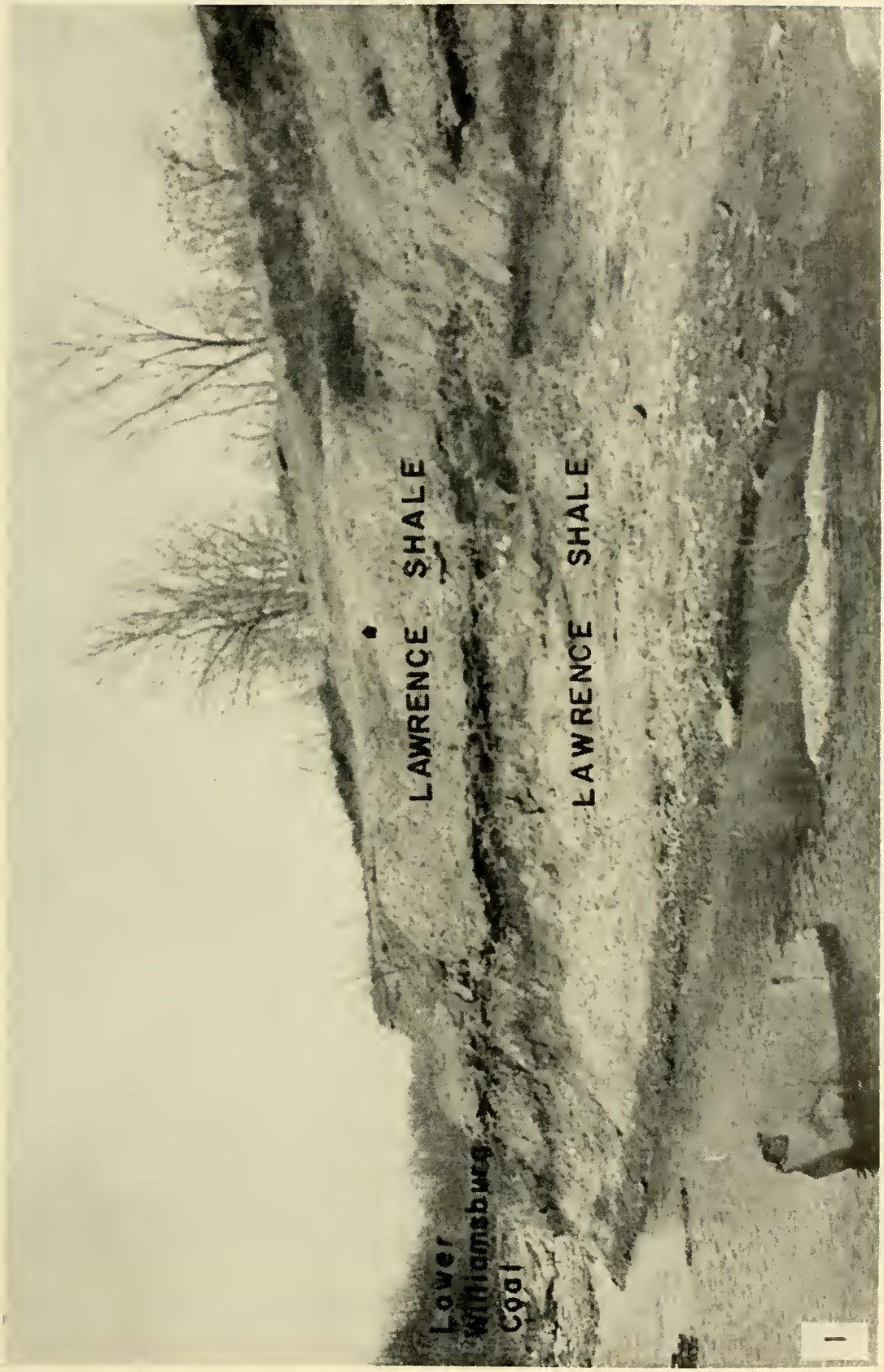


PLATE 27

Outcrop of Lower Williamsburg Coal 75 yards below the Lone Star Lake Spillway in NW corner Sec. 13, Twp. 14 S., Range 18 E., Douglas County, Kansas. The coal occurs in the west bank of a tributary that runs into the Wakarusa River.

PLATE 27

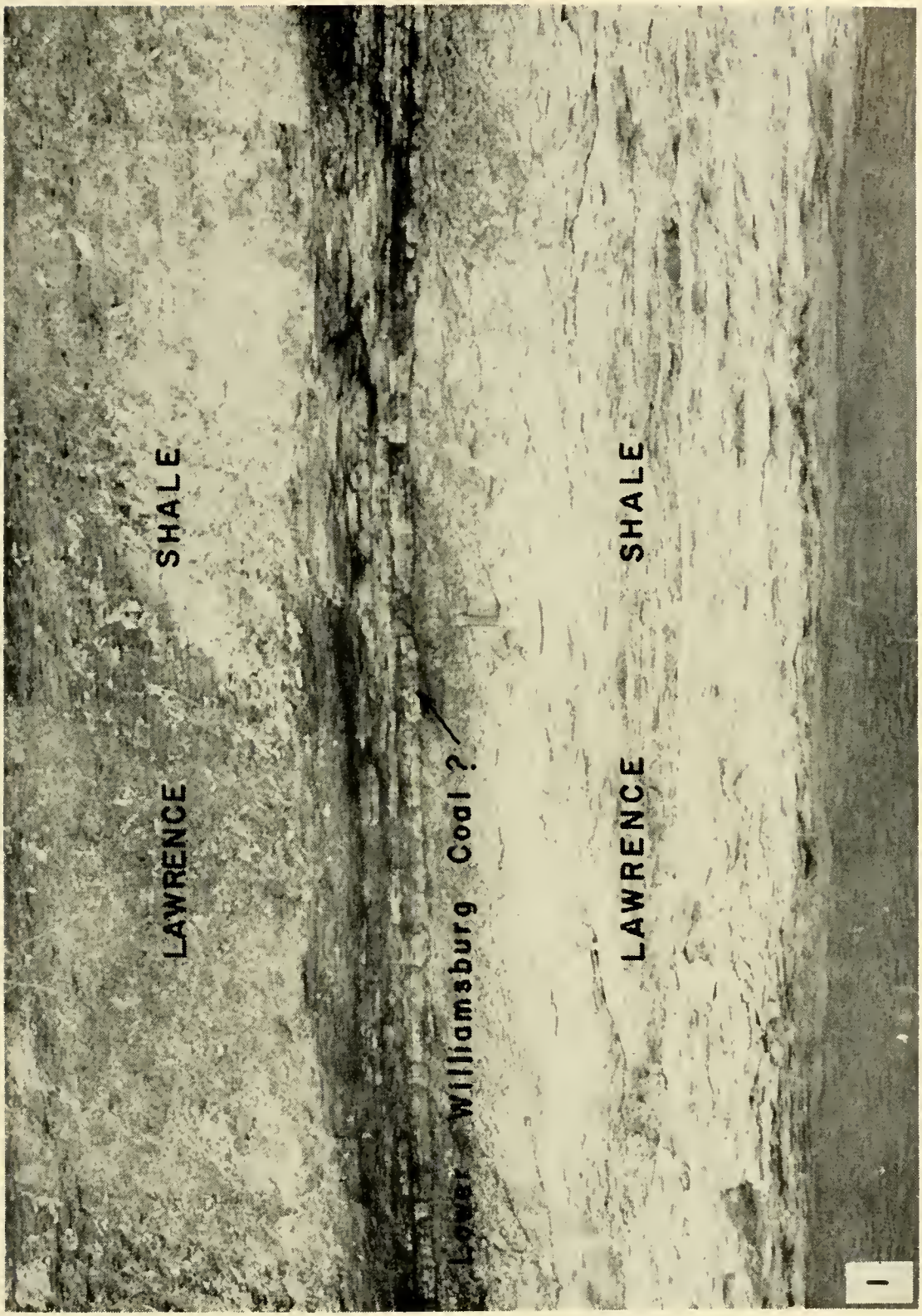


PLATE 28

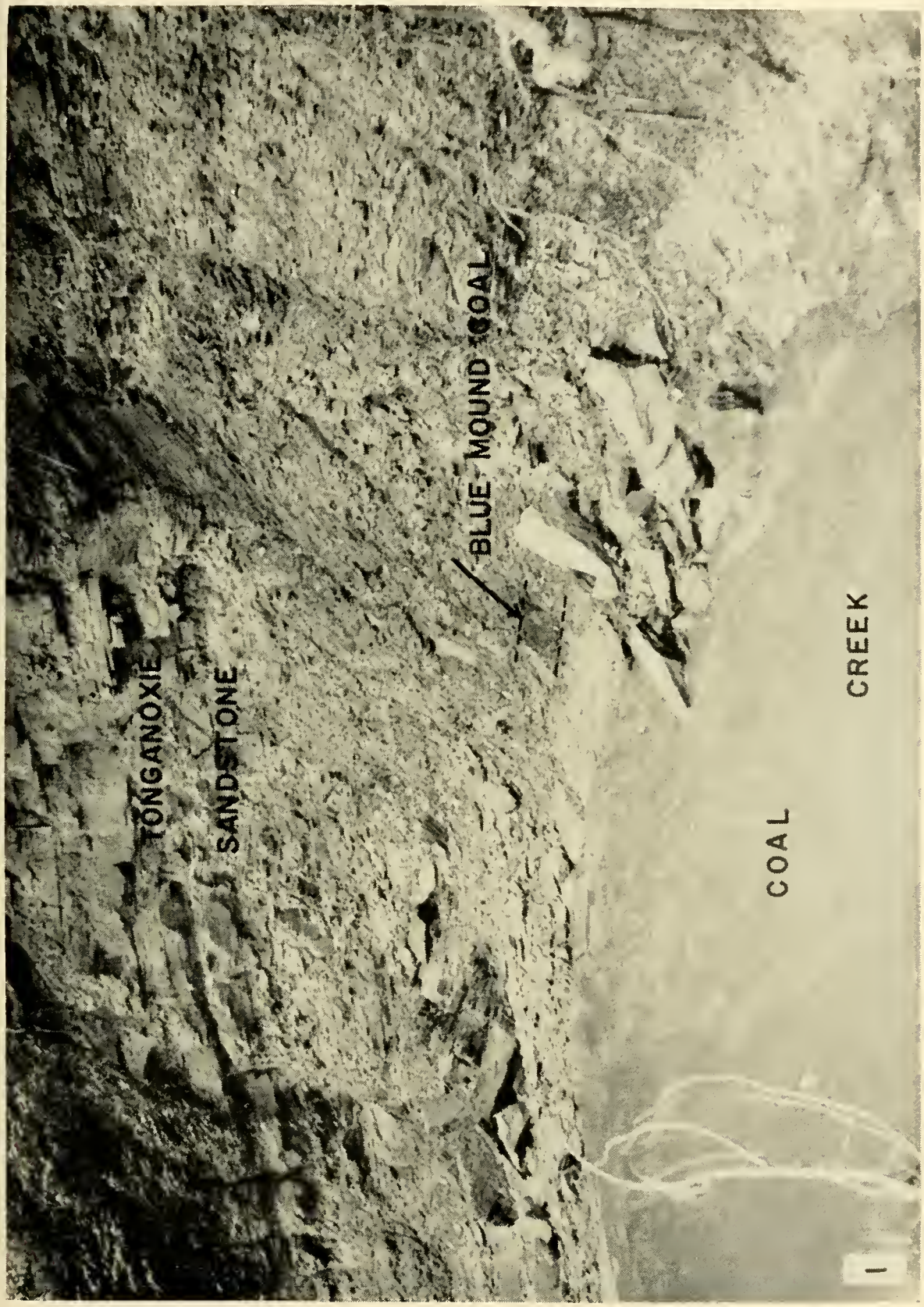
Close-up of Lower Williamsburg Coal outcrop below Lone Star Lake Spillway. The top zone is 3 inches thick, middle is 2 inches thick and the bottom is 5½ inches thick. This picture is an enlargement of the area directly above the "g" in the word, Williamsburg, on plate 27.

PLATE 28

PLATE 29

Outcrop of Blue Mound Coal in NE 20 acres of NW¼ of Sec. 28, Twp. 13 S., Range 30 E., Douglas County, Kansas. The outcrop is along the east side of Coal (sometimes called Cole) Creek. Outcrop thickness of coal was 10-11 inches. Good Compressions of *Neuropteris scheuchzeri* Hoffm., *Alethopteris, Pecopteris, Alloiopteris, Asterophyllites* and *Annularia* may be found in the Tonganoxie Sandstone, a few feet above the coal bed.

PLATE 29



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SCIENCE BULLETIN

VOL. XLII] DECEMBER 29, 1961 [No. 8

Observations on the Biology and Taxonomy of Flies Found Over Swarm Raids of Army Ants. (Diptera: Tachinidae, Conopidae)[1]

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ABSTRACT: There are three important genera of flies found over and near swarm raids of army ants (Formicidae: Dorylinae) in Panamá. These three genera are *Stylogaster* (Conopidae), and *Calodexia* and *Androeuryops* (Tachinidae). All three genera are mainly found over the area where the raiding ants are concentrated at the front of the swarm and up to two meters in advance of the swarm front. There is no good evidence that any flies are found frequently in the fan area behind the swarm front or over raid or emigration columns. When these flies from the swarm front are found in the fan area, it is usually because a specific host insect has remained there or has fled to the fan area. These flies are found neither within the nests nor running in the ant columns.

Stylogaster differs in its behavior from the other two genera by its almost constant hovering. *Calodexia* and *Androeuryops* usually rest on low objects and frequently shift position to avoid the ants. No species of *Stylogaster* has been reared, but it appears that those species found over army ant swarms are parasitic on cockroaches. This is indicated by their darting after cockroaches driven out by the ants and by the finding of at least one egg on a cockroach. However, their eggs have been found also on *Calodexia* and *Androeuryops* which may possibly be hosts for the conopids. A first instar larva of *Stylogaster* is described from an egg found on a *Calodexia*.

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Calodexia males are extremely rare near the ants, but the females are very common, over a thousand accompanying a large swarm raid. Large numbers of *Calodexia* are attracted to swarms of both *Labidus praedator* and *Eciton burchelli* at any time during daylight and twilight. These flies appear in the first ten minutes after the start of a raid, and increase to about 60 flies within a half hour. They probably locate the swarm front by the odor of the ants. Of 12 species of *Calodexia* compared, six show a significant preference for swarm raids of either *L. praedator* or *E. burchelli*. The greater abundance of these species over one or the other species of ant is probably attributable to differences in the raiding behavior of the ants. The dissimilarity in raiding results in qualitative and quantitative differences in the arthropods driven out by the ants.

Calodexia is larviparous and probably deposits larvae on the surface of a host rather than inserting them. Brief descriptions of the three larval instars are given. Larvae of *Calodexia* were found in crickets (Gryllidae) and cockroaches (Blattoidea), and a few adults were reared from these hosts. These are the most common large Orthoptera found in the litter of the forest floor.

Males of *Androeuryops ecitonis* are almost twice as abundant as females over the swarm raids of army ants. The behavior of *A. ecitonis* around the swarms appears to be similar to that of *Calodexia*, but no host is known for the species. It is oviparous and its ovipositor indicates that the eggs are laid inside the host. Unlike *Stylogaster* and *Calodexia*, the numbers of *Androeuryops* were much higher in the dry season and early rainy season than they were later in the rainy season.

All three genera are thought to find their hosts by seeing them as they run or fly to escape the ants. Apparently these flies would be unable to find hosts without the aid of the ants or at least would be much less successful at finding hosts. The combined attack by the ants and these Diptera must kill a large number of orthopterans. Possibly less than ten percent of the potential hosts within the area swept by a swarm raid escape death by either the ants or these flies; indeed, meager data indicate that 50 to 90% of the cockroaches and crickets that escape the ants are parasitized by *Calodexia* alone.

Although this study was done in Panamá, identical or related species of flies appear to be present throughout the range of the two ants with which they are associated. These ants, *Labidus praedator* and *Eciton burchelli*, range from southern Mexico to southern Brasil in areas of wet tropical forest.

A revised key to the species of *Calodexia* and partial redescriptions are included.

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INTRODUCTION

This study is the result of brief observations made on the flies found over raids of army ants from January to June, 1952, January to April, 1955, and of a more extensive survey with attempts to study the biology of these flies from February to August, 1956. The Canal Zone Biological Area was selected as the site for this study for reasons of convenience and especially because Dr. T. C. Schneirla and his associates have investigated the behavior of the army ants in this area intermittently since 1932. References to their earlier papers and summaries of the behavior of army ants are given by Schneirla (1956, 1957a, 1957b).

The Canal Zone Biological Area is a wildlife preserve including

the entire area of Barro Colorado Island. This island has an area of about six and one-half square miles and is located approximately in the center of the Canal Zone. Except for a few small clearings and limited areas of second growth, the entire island is covered with evergreen seasonal forest, an intermediate formation, in the classification of Beard (1944), between true tropical rain forest and semievergreen or deciduous seasonal forest. There is a well-defined, but not too severe, dry season from about January to April when the leaf litter becomes dry, the clayey soil cracks, and some of the trees lose their leaves. A graph of mean monthly rainfall for 1925 to 1939 is given by Schneirla (1949: 12). The months of January and April are quite variable and can be considered dry or rainy season depending upon the year. Since there were 5.57 inches of rain in January of 1956, including over two inches in the last week of the month, one should not consider this month as part of the dry season for that year. In February, March, and April between 2.1 and 2.6 inches of rain fell in each month, which is slightly above the average precipitation, and the relatively even distribution of the rain made the 1956 dry season a moderate one.

Additional information on Barro Colorado Island and its ecology has been presented by Allee (1926a, 1926b), Enders (1935), Kenoyer (1929), Moynihan (1959), Williams (1941), and Woodring (1958).

Neotropical Army Ants and Their Types of Raids

In order to explain the role of the flies during the raids of the army ants a brief outline of the biology of the ants is essential. The term "army ants" has been used to refer to any species of ant which raids by groups of workers; however, it usually refers to members of the subfamily Dorylinae which are the most conspicuous group-raiders in both the Old and New World tropics. As used in this paper the term refers only to this subfamily. Most dorylines are small, inconspicuous ants which nest and raid underground, but often come out on the surface at night or on humid, cloudy days. All species are predaceous and feed almost exclusively on living arthropods which they capture during mass expeditions or raids. With rare exceptions indicated later, only the species which forage in "swarm raids" (Schneirla, 1934, 1940) are accompanied by the flies discussed in this paper.

There are only two species of army ants in the Western Hemisphere which make swarm raids, *Eciton burchelli* (Westwood) and *Labidus praedator* (F. Smith) (*Eciton praedator* of authors). *E.*

burchelli ranges from Southern Mexico to Southern Brazil in areas of wet tropical forest. The distribution of *L. praedator* apparently overlaps that of *burchelli* almost completely and also extends beyond it into slightly drier areas. Scattered reports from throughout the Neotropics indicate that the species have similar swarm raids wherever they are found.

SUMMARY OF THE BIOLOGY OF THE SWARM RAIDERS WITH EMPHASIS ON FACTORS INFLUENCING RAIDING

E. burchelli is an epigaeic species both in nesting and in raiding. Its temporary nest or bivouac is usually located under a fallen log, in a hollow tree or log, between the buttresses of a tree, or in a brush heap. The bivouac is a cluster of 500,000 to 1,500,000 worker ants hanging from some support which usually shelters the ants at least partially from above. The single queen and the one or two immature broods are in the more central parts of the bivouac. Schneirla has shown the developmental stage of the brood is of major importance in regulating an alternating cycle of statary and nomadic phases. During the nomadic phase of 12 to 15 days, a *burchelli* colony has a single brood of usually 100,000 to 300,000 worker-producing larvae. At this time there are large daily raids followed by an emigration every night to a new bivouac site. When the brood spins cocoons, the colony enters the statary phase in which its bivouac remains at one site for about 21 days. During a seven- to 12-day period near the middle of this phase the queen lays another brood of worker-producing eggs. Thus, during the latter half of the statary period there are two broods present in a colony. The emergence of the young callow workers triggers larger daily raids and the emigration that starts a new nomadic phase (Schneirla, 1957a).

Labidus praedator seems to have a similar nomadic-statary cycle, but scattered observations indicate that the broods are not as closely synchronized, and the colonies may not emigrate nightly throughout a distinct nomadic phase. Since the bivouacs are all underground or in well-protected places, such as inside rotten logs, it is seldom possible to determine the type of brood or even find a nest. Raids and emigrations can be found on the surface of the ground, but apparently a large part of the raiding and possibly the entire emigration route may be subterranean.

THE SWARM RAID

One of the most impressive sights in a tropical forest is a large swarm raid of army ants. These raids are so spectacular that they have been described repeatedly by both naturalists and casual travelers since they first were discovered. One of the earliest and most accurate of the older accounts of such raids in tropical America was by Bates (1863) who is apparently the first to give a clear account of the complex of birds and arthropods which accompany the swarms of ants. In addition to from 50,000 to perhaps 300,000 ants running rapidly over the forest floor, there is the stampede of insects and other animals escaping the jaws and stings of the ants. Conopid flies of the genus *Stylogaster* hover over the ant swarms. A large swarm may be accompanied by over a thousand Tachinidae, which dart from leaf to leaf and dash after Orthoptera escaping in front of the advancing ants. Hundreds of other flies, mainly belonging to the families Muscidae and Sarcophagidae, add to the confusion. A single sweep of a net with a diameter of 40 cm. will easily trap about 25 flies under good conditions. The combination of the buzzing of insects in flight, the running of the ants and the fleeing arthropods among dried leaves, punctuated by the larger snaps from jumping Orthoptera, adds up to the distinctive and quite audible sound of a swarm raid of army ants. On at least two occasions I have found army ant colonies which were a short distance away from a human trail on Barro Colorado Island by the noise of these arthropods. Curran (1934a: 1) stated that the flies "create a buzzing that may be heard for a distance of more than twenty feet. In every case in which I located armies of ants I was attracted by the noise of the flies."

Furthermore, a well-developed swarm raid is accompanied by the antbirds which also add to the excitement and noise. A brief study of the behavior of these antbirds has been completed by Johnson (1954), but much basic information on them is still lacking. Most of the antbirds apparently do not eat the ants but feed on spiders, cockroaches, and other arthropods escaping from the ants. Even on this basic point, however, there is contradictory evidence. Although it is impossible to learn what these birds are eating without examining stomach contents, one would expect that they would eat the flies near the swarms since the birds seem to eat mainly insects flying up from the ground.

A brief outline of the development of a raid of *Eciton burchelli* is given below, with emphasis on those aspects related to the flies.

Although the behavior of the ants has been extensively studied by Schneirla (1934, 1940), the numerous and diverse animals which are associated with these raids have been largely ignored.

A maximal raid typically occurs near the end of the nomadic phase and starts at dawn when it is barely light enough for an observer to see the ants. The workers leave the nest at first in small numbers, spreading out in all directions. Larger numbers soon pour out mainly in the directions of easiest exit, such as along branches or lianas which may be part of the bivouac support. On the few occasions when the start of a *burchelli* raid was observed at dawn the flies began to appear within the first ten minutes. As the workers fan out in an advancing arc, there is constant movement in both directions along the continuous column connecting the raid front and the bivouac. The only time in the course of an army ant raid that the ants at the swarm front may not be connected with the bivouac by a relatively continuous column is during a sudden rain, or to a lesser extent during the "siesta period." A strong basal raid column is normally two to four centimeters wide near the bivouac with ants passing any one point at the rate of about 50 in seven seconds. Usually within a half hour of the start of a raid, the mass of milling, advancing ants has narrowed down to one or two advancing swarm fronts. There is no "advance guard" or group of pioneering workers at the front of the swarm. The composition of the swarm front is constantly changing; ants from the rear run forward, those in front run backward, some returning to the rear with booty. As they advance across the forest floor, the ants flush out a vast number of spiders, scorpions, amphipods, and other animals, both vertebrate and invertebrate. The Neotropical army ants are not as vicious, from the standpoint of attacking and killing vertebrates, as are the African species of *Dorylus* (*Anomma*). However, *burchelli* will flush out mammals from their burrows or resting places and occasionally will kill a snake, lizard, or other small vertebrate.

No one has studied any species of Dorylinae to determine what animals are commonly captured or to estimate the proportion of potential prey that escapes from the ants. The popular statement that they kill all animals is far from the truth, although they will attack most species in the path of the swarm. Some species of arthropods are clearly avoided, and others appear to be overlooked or cannot be attacked successfully because of protective adaptations. Even among those animals which the ants often capture and eat,

there is a large proportion which escape. Casual observations indicate that this proportion which escapes may be between 30 to 50 percent. This percentage obviously fluctuates widely depending on the size of the raid and the species of prey involved.

The direction and distance that a raid progresses seems to be influenced mainly by the nature of the terrain and by the abundance of booty in particular areas. If, for example, a large colony of carpenter ants is found at one side of the swarm, the raiding ants will be drained away from the center toward that side. In this manner an advancing swarm front may shift direction or be divided into two sections. Essentially all the attacking of prey takes place in a limited area at the front of the swarm. This area extends from the leading edge of the swarm back toward the bivouac for from one-half to two meters. In this area the ground seems to be largely covered by thousands of ants running in all directions but maintaining a steady advance. Behind this swarm front there is a fan-shaped area of anastomosing columns leading back to one base column extending to the bivouac.

The maximal development of a *burchelli* swarm raid usually is seen between 10:00 and 11:00 a. m. when the swarm front may be 100 to 200 meters from the bivouac and 10 to 15 meters wide. Usually between 11:00 a. m. and 3:00 p. m. there is a decrease in raid intensity called the "siesta period" by Schneirla. During a maximal raid some raiding usually continues through this period, but the front is weaker, making little progress, and most activity consists of killing and pulling apart the booty which has been attacked earlier. Normally an increase in raiding activity starts between 3:00 and 6:00 p. m., and the greater exodus from the bivouac at this time gradually changes into an emigration of the colony, if it is in the nomadic phase. At times a *burchelli* raid may continue well after dark, until about 9:00 p. m., with the emigration starting after that time or while raiding is still going on at the front.

Raids of *burchelli* colonies which are below the maximal type outlined above differ in the following ways: They may begin late in the morning or even in late afternoon, but they apparently never start during the siesta period. A minimal raid may consist of a swarm about one meter wide advancing only four or five meters from the bivouac. Occasionally, *burchelli* may have weak swarms less than a meter wide which further decrease as they advance away from the bivouac and soon appear like the column raids of *Eciton*

hamatum. At the front edge of a *burchelli* swarm raid there are short pseudopodic columns rarely extending more than 10 to 20 cm. beyond the body of the swarm. However, when the raid is interrupted by rain, or stops for any reason, the edges of a *burchelli* swarm raid can look very similar to a column raid. Nevertheless, even at these times more flies are seen near the *burchelli* than are seen near column raids of *hamatum*.

The *Labidus praedator* raid pattern is very similar to that of *burchelli* but has several fundamental differences. The amount of raiding activity on the surface of the ground seems to depend largely on the humidity, since *praedator* clearly is found more frequently after rains and especially in the rainy season. I have not seen the start of a *praedator* raid. Presumably they start like those of *burchelli* but on a smaller scale, since the swarm front seldom exceeds three meters in width. As the swarm front advances, it changes direction more frequently than does the front of a *burchelli* raid. At times a *praedator* raid will turn in a circular or spiral pattern, going back over much of the same area raided only a few minutes before. As the *praedator* swarm advances, the anastomosing columns connect with a base column which remains underground. The points where these columns go underground may be progressively changed as the swarm advances, and these holes presumably get farther from the bivouac and stay relatively close to the swarm front. This is the primary reason why it is usually impractical to locate bivouacs of *praedator* by following the base column back in the direction that the ants are carrying booty, and digging where the column goes underground. This point may be ten or more meters from the bivouac. Some *praedator* base columns and emigration columns may extend more than 150 meters on the surface of the ground. Because it is so difficult to pinpoint the location of a *praedator* bivouac and to follow the raiding of the same colony on subsequent days, only about one-half as many *praedator* raids as *burchelli* raids were studied.

Diptera Associated with the Swarm Raids

The family Phoridae has long been known to contain numerous myrmecophiles, many of which have been found only with species of army ants, including *burchelli* and *praedator*. They are the most common myrmecophiles found *in the raid columns* of both *burchelli* and *praedator*, but it has not been possible to determine whether these flies all had left the bivouac earlier, or whether they had

found the swarm or a raid column and then followed the columns back toward the bivouac. At the end of a *praedator* raid, as the ants are retreating down a hole in the ground, I have on a few occasions seen several hundred phorids running among the ants or following after them. Rarely, winged phorids can be seen flying over columns, and it is likely that these are males searching for the normally wingless females. As Phoridae are not ordinarily taken flying about the swarm raids, they are not considered further at this time.

Among the Diptera that can be collected by sweeping over swarm raids there are numerous families which have no apparent association with the ants, such as the Callobatidae, Chloropidae, and Syrphidae. These can be collected in approximately the same numbers by sweeping close to the ground and through the low vegetation in any area of the forest. The family Calliphoridae, on the other hand, appears to be somewhat more abundant over the ant swarms, and the families Sarcophagidae, Muscidae (Anthomyiidae), Conopidae, and Tachinidae are clearly much more abundant than in neighboring areas of the forest where the ants are not present (excluding areas with obvious attracting substances such as dead animals or rotting fruit). It is possible that some of these flies are attracted to the noise, odor, or appearance of other flies flying over the ant swarms, rather than to the ants themselves. I suspect this may be true of the Callophoridae, some Sarcophagidae, and some Muscidae. There are other species in the last two families, however, which seem to be associated with the ants, and these will be discussed in a later paper after the species have been described. At least three species of Muscidae, which are attracted to the swarms, breed in remains of booty deposited by the ants outside their nests. These flies may locate a swarm and then follow the ant columns back to find the bivouac. These muscids are relatively rare at the swarm front but common at the bivouacs. Such forms are not discussed further in this paper, the following discussion being limited to Conopidae and Tachinidae.

The Behavior of Stylogaster

The genus *Stylogaster* can be readily distinguished from all other Conopidae by the greatly elongated abdomen and ovipositor indicated by the generic name. The genus is so distinctive in this and other respects that Williston (1885: 388) placed it in a separate subfamily where it has remained as the only genus ever since. The

most recent or important taxonomic papers on *Stylogaster* are by Aldrich (1930), Lopes (1937), Kröber (1940), Séguy (1946), Camras (1955, 1958), and Lopes and Monteiro (1959). References to other taxonomic literature can be found in these papers.

The genus is found in North and South America, Africa, and Asia. About 45 species have been described, but published reports are limited almost entirely to the original descriptions based mostly on few specimens. There are about 15 species known from Africa and Asia, and all are considered distinct from those in the New World. In America the genus ranges from Massachusetts to Bolivia and Argentina. In no locality has this genus been reported as abundant except over swarm raids of Dorylinae. There are scattered records of *Stylogaster* being taken at flowers, and one species, *macrura,* was taken at light (Lopes, 1938: 405). In Africa four people have reported seeing *Stylogaster* hovering over "columns" of *Dorylus (Anomma)* [probably *nigricans* or *wilverthi* in all cases] (Brauns in Bequaert, 1922: 282; Bequaert, 1930: 167; Carpenter, 1915: cviii-cix; and Cohic, 1948: 271). (No determination of the insect seen by Carpenter was given, but from its description it presumably was a species of *Stylogaster.*) It is interesting to note that Brauns, Bequaert, and Cohic all reported that the fly was seen hovering over *columns* of the driver ants. It is likely that these observers did not distinguish the basal columns and the swarm front sections of a raid in the sense of Schneirla, but called the entire raid a column. It is important for observers to distinguish between the swarm front, basal columns, and emigration columns since there is some evidence that different flies either prefer or are restricted to these dissimilar aspects of the behavior of the ants.

In my observations in Panamá, *Stylogaster* was usually seen over the densest areas of the swarm front or in advance of the swarm front by one to two meters. This conopid was occasionally seen over the area of anastomosing columns slightly behind the swarm front but never over the basal columns. *Stylogaster* was present over every maximal swarm observed, but it was not found over a few smaller swarms. Wheeler (1921: 295) and Mann (in Aldrich, 1930: 4) also reported that the species of *Stylogaster* hovered over the swarm front and apparently not over the columns behind the front. However, Curran (in Aldrich, 1930: 5) stated, "The flies (*Stylogaster*) were observed to hover over any part of the moving column, and thus differed from the other flies associated with the ants. The Tachinids . . . were almost invariably found near or in front of the head of the column. . . ."

Stylogaster, by its habitual hovering, could be distinguished from all other flies associated with the swarm raids. At times it would hover for as long as several minutes in one spot and then dart a few centimeters are more than a meter away where it continued to hover. The *Stylogaster* species are all difficult to see because of their dull coloration, thin bodies, and extremely rapid movement. Consequently, in the dim forest light, specimens often were lost from view as they shifted from one spot to another. On rare occasions a *Stylogaster* was seen perched on vegetation over the swarms, as was reported also by Lopes (1937: 260). However, it is impossible to state the frequency with which species of *Stylogaster* rest on vegetation because of the difficulty in finding these motionless flies.

While hovering 30 to 70 cm. above the ground, females of *Stylogaster* characteristically flipped their abdomens down, or their whole body shifted downward a few centimeters. This movement suggested that the flies were dropping or shooting eggs at the ants below. However, there is no positive evidence that they were ovipositing, and at times it was certain that they were not aiming at any insect, because they continued this behavior over vegetation or bare ground where no insect could be seen. *Stylogaster* was never seen to dart at the ants alone. However, on several occasions it was seen to dart after cockroaches, each of which was being pursued by at least five *Calodexia* (Tachinidae).

Nevertheless, on the basis of the behavior of the flies over the swarm raids three authors concluded that *Stylogaster* is parasitic on the army ants (Townsend, 1897: 23; Wheeler, 1910: 419; and Mann in Aldrich, 1930: 4). Wheeler (1921: 295) later wrote that he found a "swarm of both sexes of *Stylogaster* hovering over a spot where there were no Ecitons, although a few workers of *Gigantiops destructor* and *Ectatomma ruidum* were running about in the vicinity." He concluded that it is doubtful that the flies are intimately attached to the ants but that they may be attracted by the ants' rank odor. His statement is the only one indicating that *Stylogaster* is possibly associated with non-doryline ants, and it also is noteworthy for reporting a "swarm" of *Stylogaster*. I have never seen more than about ten scattered specimens of this conopid per hour, while watching a swarm raid.

Moreover, Mann suggested that *Stylogaster* attacked the ants in the swarm and not in the raid columns where he thought the more closely-massed workers would be more likely to kill the *Stylogaster*.

The behavior of the ants, however, indicates that insects are more likely to be attacked at the swarm front.

A further suggestion that *Stylogaster* is parasitic on the ants is also open to question. Cohic reported seeing *Stylogaster cohici* Séguy hovering several times at a height of 10 to 15 cm. and dropping eggs on columns of *Dorylus* (*Anomma*) *nigricans*. He suggested that since these eggs were picked up by the workers and carried into the nests, perhaps *Stylogaster* parasitizes the *nigricans* larvae (Séguy, 1946: 99; Cohic, 1948: 271). This would seem unlikely since all other conopids insert their eggs into the bodies of adult hosts on which they are internal parasites. Moreover, the egg of *Stylogaster* is well adapted as a piercing egg rather than an egg which would simply be dropped to be picked up by the host. Unfortunately, Cohic does not state whether he collected any of the eggs. It is possible that he assumed the *Stylogaster* were depositing eggs when he saw them flip their abdomens, and that the eggs he saw picked up by the ants were those of some other fly. Thorpe (1942) has reported seeing *Stomoxys ochrosoma* Speiser on one occasion deposit an egg in front of a worker of *D.* (*Anomma*) *nigricans* which then picked up the egg and carried it toward the nest. It would appear to be impossible to confuse adults of *Stylogaster* with *Stomoxys*, but eggs seen on the ground might be confused. The egg of *Stomoxys* was estimated as two millimeters long, more than twice the size of any known *Stylogaster* egg. The length, thinness, and yellow color of *Stylogaster* eggs make it unlikely that these were the eggs seen by Cohic. Many times in Panamá a species of Muscidae was seen laying eggs near the bivouac of *Eciton burchelli*, and these were seen to be picked up by the workers and carried into the bivouac or to refuse deposits of the ants. However, this fly was not seen to oviposit over the swarm front nor over columns except within a meter of the bivouac. A large series of specimens of this muscid was reared from the material found in the refuse deposits. No reports of similar flies have been found in the literature concerning *Dorylus* (*Anomma*).

Although Curran inferred that the conopids "normally occur singly and associate themselves with the ants as the army travels, their numbers being augumented as the column moves along," he also stated, "There is certainly a close relationship between the flies and the ants." He concluded that they neither parasitized the ants nor the cockroaches but ". . . seemed intent only on hovering in patches of sunlight over the army." However, he added that

they might oviposit on the ants *in the evening*, and the eggs would then be carried into the nests where the larvae would feed on the brood (Curran in Aldrich, 1930: 4).

It is unfortunate that Curran (1942: 62-63) amended his note published by Aldrich (1930) by stating that the ants over which he collected the *Stylogaster* in Panamá were *not* "army ants" but "ant armies" thought to be "entire colonies moving to a new home." He apparently changed this solely because the ants were "much smaller than most *Eciton*." There are no other non-doryline ants on Barro Colorado Island that Curran could have found "frequently" and in "enormous numbers" moving in swarms across the forest floor. The ants he saw must have been *Labidus praedator* in which the workers are much smaller than those of *Eciton sens. str.*, and they were undoubtedly raiding rather than emigrating.

My observations support none of the hypotheses of Curran. In watching swarm raids while they were just beginning, I have seen *Stylogaster* appear in the first few minutes when the swarm front was less than two meters from the bivouac. At other times they were not seen near the bivouac, and on more than a dozen occasions sweeping around the bivouacs yielded no specimens. Sweeping over the area where a swarm raid had completely ceased showed that the flies rapidly dispersed. Approximately a half hour after an area had been teeming with both ants and flies, not a single *Stylogaster* nor tachinid seemed to be present. This refers primarily to raids of *praedator* since this species may disappear underground in about 15 minutes, whereas a raid of *burchelli* ends more gradually. It is possible that *Stylogaster* prefers to hover in the sunlight, but I think one gets this impression because they are easier to see there. Lopes (1937: 260) also records that he saw them flying in the sunlight and resting on vegetation when the sun went behind a cloud. On many occasions I have seen them hover in shade, or move from sun to shade seemingly at random. Nevertheless, it may be true that when they are *not* accompanying the ants, they are more apt to hover in the sun. Curran saw them hovering in sunlight on several occasions where ants were *not* present. I never observed any specimens where ants were not present and took only two specimens by sweeping vegetation where no ants were seen. (We spent more time sweeping where ants were *not* present than we spent sweeping over swarms.) In this connection, Townsend (1897a: 23) reported that in collecting for three months in the State of Vera Cruz, Mexico, he saw *Stylogaster* only

on one occasion when he caught 51 specimens. These were all taken over a single swarm raid of *E. burchelli* by sweeping during the last hour or two of daylight. The number of specimens he took indicates a much higher proportion of the flies accompanying the swarm were *Stylogaster* than we found in Panamá. The ratio of tachinids to *Stylogaster*, based on the specimens listed in his papers, is about 1:1, whereas we found about 25:1.

Observations on the behavior of the flies in the evening are more limited because at that time the swarms are usually more poorly developed and thus have fewer flies near them. In addition, it is much more difficult to observe the flies in the dimmer light. On three occasions I observed *Stylogaster* and *Calodexia* near dusk apparently behaving in the same way as earlier in the day. *Stylogaster* was also seen when raids by *burchelli* were just beginning, and only a few scattered sunflecks were reaching the forest floor. On 20 February 1956, when watching one raid start from a bivouac with a brood of worker larvae, I saw the first *Stylogaster* at 7:14 a. m. when the ants had only progressed 0.5 to 1.0 m. from the bivouac. The first *Calodexia* appeared six minutes later.

The number of specimens of *Stylogaster* which we collected on Barro Colorado Island plus one record for S. *stylosa* taken by T. C. Schneirla, are recorded in table 1. The small number of specimens makes it difficult to draw any conclusions as to whether any species shows a preference for the raid swarms of either species of army ant. One would have expected to find more specimens over *burchelli* considering the greater number of swarms and longer total collecting time over this species. (Approximately 70% of the collecting time was over *burchelli*.) This difference will be discussed more under *Calodexia*. In addition to the species listed in table 1, the following species have been collected in Panamá by C. H. Curran, N. Banks, S. W. Frost, and R. C. Shannon: *apicalis*, *ethiopa*, and *indistincta*. All the Panamanian species were described by Aldrich (1930) except for *ethiopa*, *minuta*, and *stylosa*, which were described by Townsend (1897a). Most specimens of all species from Central and South America have apparently been taken over army ants, but only two authors have given determinations for both the ants and flies. Those known from over *L. praedator* in Brazil according to Lopes (1937) are: S. *australis* Lopes, *ornatipes* Kröbor, *rectinervis* Aldrich, *stylata* Fabricius, and *tarsata* Lopes. These species are all different from those found over *praedator* in Panamá. The three species described by Townsend were based on

TABLE 1.—Summary of Stylogaster Collection Records

TAKEN NEAR ANT SPECIES	Species of *Stylogaster*													Totals			
	banksi			*currani*			*minuta*			*panamensis*	*speciosa*		*stylosa*				
	♂	♀	?	♂	♀	?	♂	♀	?	♀	♀	?	♂	♂	♀	?	T
L. praedator	4	7	1	1	3	....	7	4	....	.....	5	.....	.....	12	19	1	32
E. burchelli	9	8	1	6	8	1	3	9	4	2	1	1	1	19	28	7	54
E. hamatum	....	....	....	....	....	....	....	2	....	.....	.....	.....	.....	....	2	....	2
E. vagans	....	....	....	1	....	....	1	....	1	.....	.....	.....	.....	2	....	1	3
Not near ants	....	....	....	1	1	....	....	....	....	.....	.....	.....	.....	1	1	....	2
Totals	13	15	2	9	12	1	11	15	5	2	6	1	1	34	50	9	93
Both sexes	30			22			31			2	7		1				93

a total of 51 specimens taken over a single swarm of *E. burchelli* in Mexico. These three species have also been found over *burchelli* in Panamá (with the possible exception of *ethiopa* where the species of ant was not given).

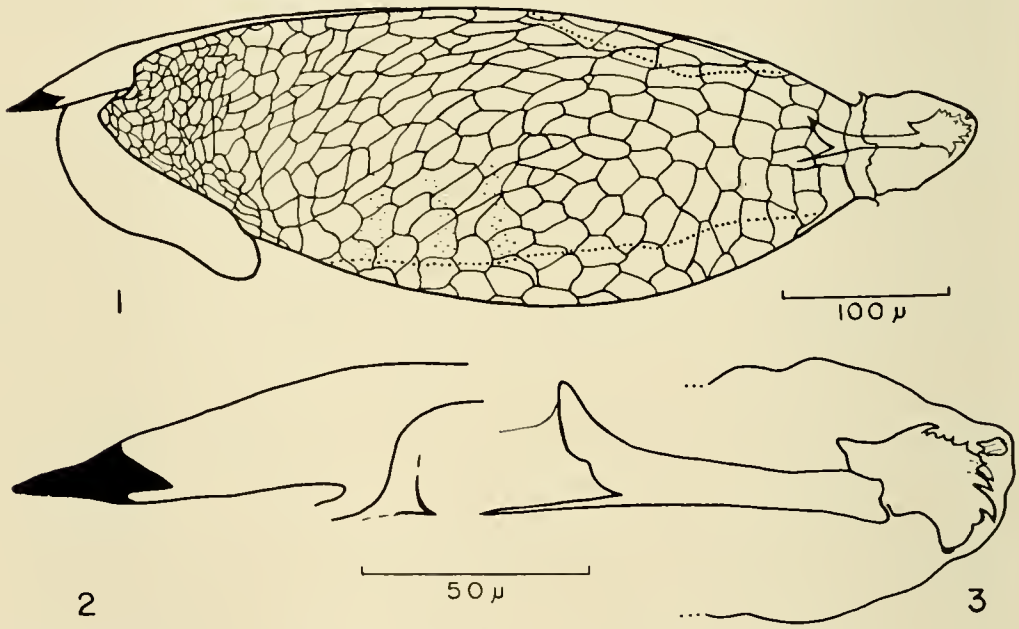
Table 1 shows a total of five specimens taken near *Eciton hamatum* or *E. vagans,* both of which raid in columns. The two females taken near *E. hamatum* were observed on 10 March 1955, hovering under a log next to the statary bivouac of colony '55 H-E. Both hovered for a few seconds only 6 to 12 cm. over the ants on the ground next to the bivouac, then shifted to another spot 10 to 20 cm. away so quickly that I could hardly follow them. The flies were not seen to dart at any of the ants, and no eggs were seen to leave the ovipositor (though they might have been missed because of their small size). *Stylogaster* was never seen near any other bivouac of *E. hamatum* even though more than 50 nests of this species were watched for brief periods or for several hours. Furthermore, I had pulled many of these bivouac apart in order to take samples of the brood and myrmecophiles. Following such a disturbance thousands of ants would be milling around the area of the nest, and the odor of the colony would be noticeably stronger. There are no published records of *Stylogaster* near *hamatum.*

On 9 July 1956, I disturbed a bivouac of *E. vagans* which had a brood of reproductives approximately at the midpoint of their larval development. Twenty-five minutes were spent thoroughly examining the bivouac and taking the queen and a large sample of the brood and workers. When this was completed, I noticed that about 50 *Calodexia* and *Stylogaster* had been attracted to the mass of *vagans* milling on two or three square meters of ground around the nest. From 10:50 to 11:20 a. m. before I attacked the bivouac, I had watched the raid which had an unusual swarm front of about two square meters quite densely covered with ants. During this time two *Calodexia* and one other fly were seen, but no *Stylogaster.* Following the attack on the bivouac, I swept over the ants milling around the site from 11:45 a. m. to 12:15 p. m., and took three *Stylogaster* and 18 *Calodexia.* Since normally *vagans* is a column raider, the unusual swarm at the head of the raid column was possibly due to the fact that this colony was stimulated to unusual activity by the sexual brood. The fact that the distal end of the raid was also only about ten meters from the bivouac may account in part for the swarm. Otherwise such flies have not been found associated with column raiders but only with the swarm raiders *burchelli* and *praedator.*

These last two cases indicate that *Stylogaster* apparently finds the ants by their odor and can locate at least four species of Dorylinae in this way. This conopid probably is attracted to many colonies but stays only with *praedator* and *burchelli* which mantain swarm raids. This can be considered additional indirect evidence against the hypothesis that *Stylogaster* is parasitic or predaceous on the ants. *E. vagans* and *hamatum* are as big or bigger than *burchelli and L. praedator* and should be just as suitable as hosts.

THE LIFE CYCLE OF STYLOGASTER

Although no larvae have been described for any species of *Stylogaster,* the eggs of most Neotropical species have been illustrated and described by Lopes (1937) or Lopes and Monteiro (1959). Lopes was the first to show that the eggs have a number of reliable specific characters which alone are sufficient for determining the species. The most outstanding characters of the egg are the shape of the pointed end, the number of recurrent spines (one to four) and the shape of a bladder-like protuberance near that end, and the pattern of reticulations on the surface (figure 1). Because of their value



FIGURES 1 to 3. Egg of *Stylogaster currani* Aldrich with larva protruding from blunt end; egg found on base of wing of *Calodexia venteris* Curran female (2341-C).

FIGURE 1. Entire egg with anterior end of larva protruding; three ventral bands of small spines and part of larval body wall can be seen within chorion.

FIGURE 2. Large spine at posterior end of egg showing one large, dark, recurrent spine near tip and one smaller recurrent spine near base of large spine.

FIGURE 3. Buccal armature and anterior end of larva; small structure anterodorsal to oral hooks is probably antenna; (only right half of larva illustrated).

in determining females which are in poor condition, as well as for determining eggs found on possible hosts, it is hoped that future descriptions of *Stylogaster* females will include descriptions of the eggs.

Stylogaster eggs are most easily removed through the ventral, membranous part of the abdomen while it is still soft shortly after collecting. However, they can also be recovered from dried specimens, though it is often impossible to avoid breaking off the abdomen because of its rather weak attachment to the thorax. The eggs which I examined were partially cleared in a clearing solution modified from that of Nesbitt (1945: 141): 40 g. chloral hydrate, 25 ml. water, 2.5 ml. hydrochloric acid, and 2.5 ml. glycerin. They were then mounted in Hoyer's medium made by the formula given by Baker and Wharton (1952: 10): 50 g. distilled water, 30 g. clear crystals of gum arabic, 200 g. chloral hydrate, and 20 g. glycerin. Clearing in clove oil, cedar wood oil, or xylene followed by mounting in balsam, diaphane, or permount was more time consuming, and the greater permanence of the slides is apparently the only advantage. These latter techniques also require more complete clearing to show the reticulation of the chorion.

All the eggs found in *Stylogaster* females had completed chorions, and eggs in earlier stages of development were not seen. This is in marked contrast to *Calodexia* in which larvae and eggs in various stages of development are found in the adult females. The maximum number of eggs in any one female seems to be between 60 and 80. Lopes (1937: 266) reported 60 in S. *stylata* in Brazil. Neither Lopes nor I found any eggs, either in females or on other insects, showing any sign of larval development except for the one discussed below.

Lopes described an egg of S. *stylata* which he found inserted between the fourth and fifth terga of an undetermined orthopteran. This orthopteran was escaping from a raid swarm of *L. praedator* above which *Stylogaster* had been seen hovering and dashing after cockroaches and other Orthoptera (Lopes, 1937: 259-260, 267-268). Later he reported that when examining the collection of cockroaches at the Instituto de Biologia Vegetal in Rio de Janeiro, Dario Mendes found a *Stylogaster* egg between terga near the end of the abdomen of an adult *Chorisoneura* sp. The species of *Stylogaster* to which this egg belongs is not known (Lopes, 1937: 289-290). Examination of about 50 cockroaches taken on Barro Colorado Island revealed no *Stylogaster* eggs; however, only about

TABLE 2.—Stylogaster Eggs Found on Tachinidae

FIELD NUMBER	Species of *Stylogaster*	Species of Tachinidae	Location of egg on Tachinid
2341–A	*banksi*	*C. dives* ♀	Lateral, between terga II and III
1755–A	*currani*	*C. agilis* ♀	Lateral, between terga II and III
2329–A	*currani*	*C. agilis* ♀	Lateral, between terga I and II (see fig. 4)
2329–B	*currani*	*C. agilis* ♀	Ventral, between terga I and II
2341–B	*currani*	*C. agilis* ♀	Ventral, between terga II and III
2242–J	*currani*	*C. dives* ♀	Thorax, slightly anterodorsal of wing base
2341–C	*currani*	*C. venteris* ♀	On wing near base, first instar larva in egg (see figs. 1–3)
2201–A	*currani*	*C. interrupta* ♀	Dorsum of ovipositor
1171–A	*minuta*	*A. ecitonis* ♀	Dorsolateral, between terga II and III
1446–C	*minuta*	*C. agilis* ♀	Ventrolateral part of eye (see fig. 5)
1854–A	*minuta*	*C. agilis* ♀	Dorsolateral part of eye
2257–F	*minuta*	*C. fumosa* ♀	Dorsal, between terga I and II
1446–G	*minuta*	*C. panamensis* ♀	Dorsolateral part of eye
1411–A	*speciosa*	*A. ecitonis* ♂	Pteropleuron, just below base of wing
1172–A	sp. a	*C. agilis* ♀	Lateral, between terga II and III
1446–F	sp. a	*C. dives* ♀	Lateral, between terga III and IV
1277–B	sp. a	*C. interrupta* ♀	Lateral, between terga II and III

ten of these cockroaches were found near army ant raids where *Stylogaster* was present.

After our return from Panamá, the examination of the tachinids associated with the swarm raids revealed eggs of *Stylogaster* on several species of *Calodexia* as well as on *Androeuryops ecitonis* (Townsend). A total of 1802 *Calodexia* and 531 *Androeuryops* were examined and 17 *Stylogaster* eggs were found, one per fly. Thus, less than 0.8% of the tachinids had *Stylogaster* eggs on them. A summary of these records is given in table 2. Of the 17 eggs found on tachinids, seven are *S. currani* and five are *S. minuta.* These are two of the most common species of *Stylogaster* found (cf. table 1). However, *S. banksi,* one of the most common adults, was represented by only a single egg. The significance of these data is subject to considerable doubt. At least most of these tachinids are large enough to serve as hosts but *Calodexia fumosa, C. panamensis,* and *A. ecitonis* would appear to be too small. However, the *Stylogaster* eggs on these three tachinids all belong to *minuta* which is the smallest of the species involved. This correlation in size may indicate that the small species of the tachinids and *Stylogaster* parasitize the same host (which may be smaller than the hosts of the larger flies), and that the *Stylogaster* lays some eggs on tachinids by mistake.

It is also noteworthy that of the 17 eggs, 7 were found on *Calodexia agilis* and 3 on *C. dives.* The incidence of eggs on these two tachinids is clearly much higher than would be expected if the eggs were laid at random on the flies. (The number of specimens for each species of tachinid is given in table 3.) Here again, the distribution of the eggs may be explained if the tachinids parasitize the same host as the *Stylogaster.*

The position of some of the *Stylogaster* eggs indicates that they may have been inserted accidentally into the tachinids. (See figures 4 and 5.) For example, several were found on eyes or wings. Nevertheless, in ten of the 17 cases, the eggs were found in the intersegmental membranes between abdominal terga. This is the same relative position as the two eggs reported by Lopes on Orthoptera. All the eggs were firmly implanted in the tachinids. Those in the eyes were inserted below the level of the recurrent spines on the sides of the eggs, the ones in intersegmental abdominal membranes were usually implanted for one-third to one-half their lengths. It would appear likely that if the eggs were accurately placed in a membranous area, they might penetrate completely in-

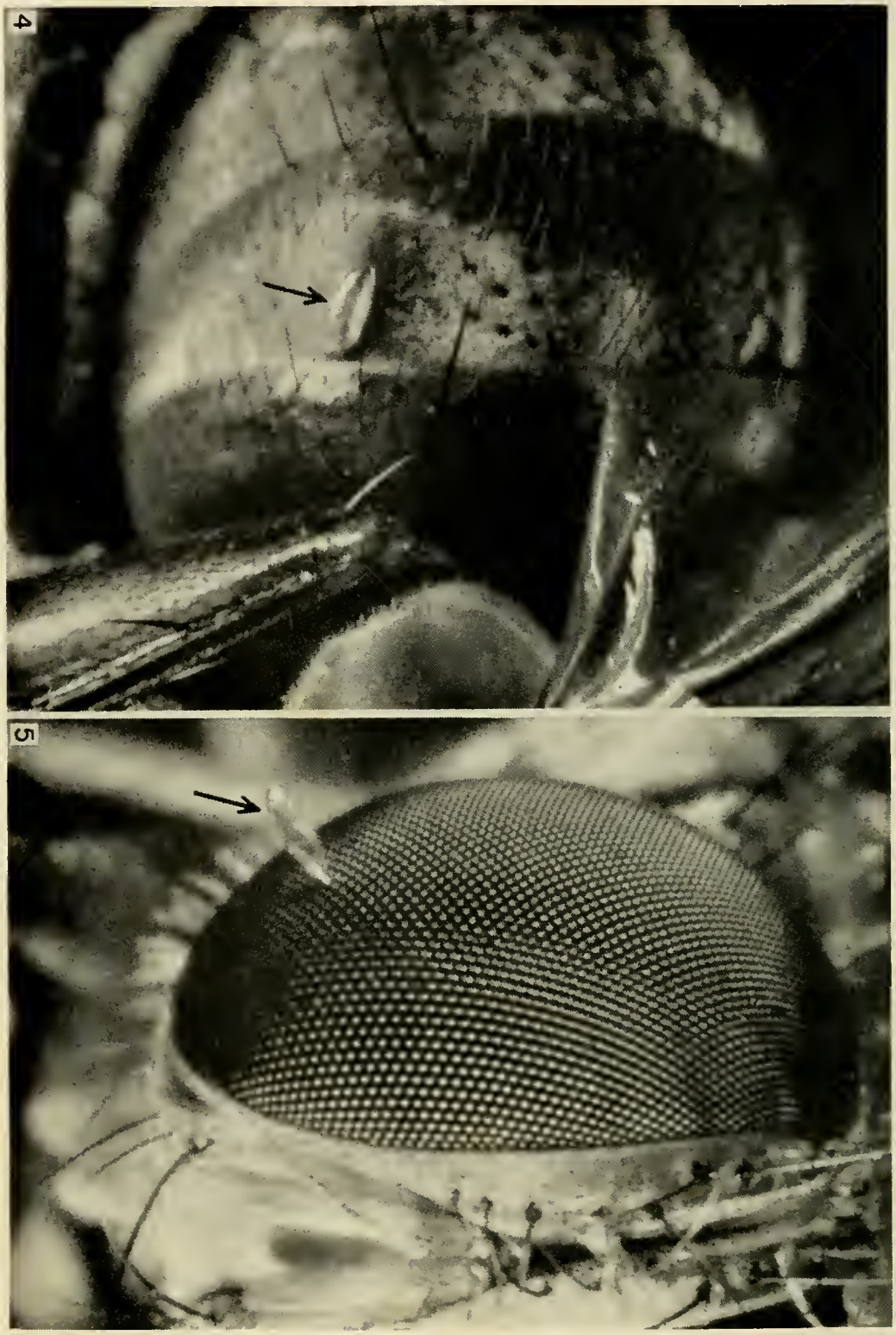


FIGURE 4. Egg of *Stylogaster currani* Aldrich inserted in membrane between first and second abdominal terga on right side of *Calodexia agilis* Curran female (2329-A).

FIGURE 5. Egg of *Stylogaster minuta* Townsend inserted in ventrolateral part of eye of *Calodexia agilis* Curran female (1446-C).

side these insects. Judging from the darker areas of cuticle around the sites where the eggs had penetrated the host, most of these eggs had probably been in the tachinids for several days.

Among the specimens of *Calodexia* examined there were about 20 which had abnormal abdomens. Included among these were flies with puncture wounds in the sides of terga, flies with asymmetrical bulges between terga, and flies with two terga fused together. These abnormal abdomens were all dissected, but no *Stylogaster* larvae nor internal parasites of any kind could be found in any of them.

Of the 17 eggs found on tachinids, only one egg showed development, but this was noticed only after the egg had been cleared and mounted in Hoyer's medium. This egg contained a first instar larva emerging from the *blunt* end of the egg, which thus must be considered anterior (see figures 1 to 3). Although Lopes (1937) has considered the pointed end to be anterior, the eggs are arranged in the abdomens of the females with the pointed ends directed posteriorly. This would not only be the logical orientation for oviposition, considering the shape of the eggs, but also would indicate that the blunt end is morphologically anterior, since eggs are normally arranged in oviducts in this position.

Near the pointed posterior end of the egg, a bladder is everted only after the egg is deposited, and perhaps contact with moisture or the physical stimulus of being forced into the host is necessary before the bladder will evert. Eggs removed from the abdomen of a *Stylogaster* will evert this structure after they are cleared if pressure is applied to the side of the egg. One function of this bladder must be to help hold the egg in the host. It also may be used to absorb fluid or other materials from the host necessary for further development of the embryo. Lopes (1937: 268) concluded that the larva must enter the host through this structure, but the discovery of the egg with a larva emerging from the opposite blunt end makes this hypothesis unlikely. Eggs removed from a female show no indication of a weaker area at the blunt end. However, after they have been softened and cleared, pressure on the side of the egg will cause the blunt tip to bulge out revealing a weaker region at that end. There is no distinct operculum, and the larva apparently ruptures the end of the egg with its oral hooks (possibly after dissolving part of the chorion). The end of the egg illustrated in figure 1 shows a thin, frayed edge around the opening through which the larva is protruding.

The buccal armature of the first instar larva, illustrated in figure 3, differs considerably from the few conopid larvae which have been described by de Meijere (1904), as well as from most higher dipterous larvae. These other conopid larvae, both in the first instar and in later instars, have one, two, or three large oral hooks which may or may not have small teeth on them. However, in the *Stylogaster* larva the oral hooks appear to have fused into a single hook with many large, hook-like teeth of approximately equal size. The pharyngeal sclerites (terminology of Roback, 1951) are separate posteriorly but fuse together before they articulate with the oral hook.

Three possible second instar larvae of *Stylogaster* were found under the following conditions. A cockroach, *Eublaberus posticus* (Erickson), taken in the forest, but not near a swarm of army ants, was used for an experimental introduction of about 12 larvae from a female *Calodexia venteris* Curran, on 30 July 1956. Five last instar larvae of *C. venteris* were found outside the still-living host on 5 August, but on the next day the cockroach died. Larvae were still seen within the cockroach, and therefore, it was not preserved until we were about to leave Panamá on 18 August. Subsequent dissection revealed 16 additional larvae, and three of these are thought to be *Stylogaster* (2236). (Numbers in parentheses are field numbers for specimens.) Each of these three larvae has a large median, ventral oral hook and two lateral oral hooks. Each lateral hook has about seven elongate, curved teeth which look like a reasonable development from the cluster of more blunt teeth illustrated in figure 3. These three larvae do not look like any known larvae of *Calodexia*. Each "*Stylogaster*" larva has a pair of rather simple posterior spiracles without large spiracular plates. This arrangement of spiracles would be expected in a second instar conopid larva, but other parasitic larvae also have similar spiracles. Third instar conopid larvae probably would have larger, more sclerotized spiracular plates. In addition, both the first instar and the "second instar" larvae have a pair of similar "antennae" on the pseudocephalon. No *Stylogaster* eggs were seen on the cockroach when it was examined prior to the introduction of the *Calodexia* larvae nor when it was later dissected. Two attempts to rear *Stylogaster* by introducing eggs into a cockroach, *Eurycotis* sp. (2246), and a cricket, *Ponca venosa* Hebard (2245), were unsuccessful.

In addition to evidence given above on possible hosts of *Stylogaster*, there is the incorrect statement by Brauer and Bergenstamm

(1893: 84) that Bates (1863) records *Stylogaster* pursuing termites. Bates (1863, v. 2: 366) in discussing *Stylogaster* makes no mention of termites, and it has been impossible to find any first-hand observation to support termites as a host. Bequaert (1922: 281) calls attention to this error and cites three repetitions of this mistake including the frequently cited classic paper by de Meijere (1904). Bequaert's paper has not had appreciable effect on subsequent reviews. Additional repetitions of this erroneous host record are found in works of Röder (1892: 287), Aldrich (1930: 4), Lopes (1937: 259), and Séguy (1949: 99).

The hypothesis of Townsend (1897a: 23) and other authors that the army ants are the hosts of *Stylogaster* is not supported by the behavior of the flies discussed above. In addition, examination of about 150,000 workers of *burchelli*, about an equal number of larvae and cocoons of *burchelli*, and about 25,000 workers of *praedator*, has revealed no *Stylogaster* eggs nor larvae which might be *Stylogaster*. Eggs may have been overlooked in examining these ants, but they must be very scarce if present at all. The worker ants are probably too small for the development of *Stylogaster* and development on queens or males would be impossible, since only a single queen is usually present in a doryline colony and males are only present for a brief period during the year.

No one has even suggested a host for any *Stylogaster* species which has not been found associated with ants. It is significant that the range of *Stylogaster* extends beyond the range of *Eciton burchelli* and *Labidus praedator*. This is seen most clearly in the United States where the genus can be found as far north as Massachusetts, far outside the range of any doryline ant.

In summary, it appears that the most likely hosts for *Stylogaster* are cockroaches and possibly other Orthoptera. Some species may be parasitic on Tachinidae, or the eggs found on them may be solely accidental. A seemingly less likely hypothesis would be that these eggs hatch and the larvae get on their true hosts when the tachinids parasitize the same host. The one case cited above of both "*Stylogaster*" and tachinid larvae in the same host would indicate that they are not incompatible, though the "*Stylogaster*" did not develop to maturity. The failure of all the larvae to develop in this instance is quite likely due to the large number (21 or more) of larvae in the relatively small host.

The *Stylogaster* species which are found over army ant swarms probably are not absolutely dependent upon the doryline ants in any

way. However, it appears that their association with the ants gives them a major advantage in finding their hosts. Without the ants to flush out the Orthoptera, *Stylogaster* would apparently have to be present at the moment when a potential host runs from cover. Some species of *Stylogaster* might be unable to find their hosts because of the secretive nature or nocturnal habits of cockroaches. However, the *Stylogaster* species which are not associated with ants, such as the species found in the United States, may be parasitic on Tachinidae or Orthoptera which are more easily found.

Androeuryops

Townsend (1897b) described the tachinid, *Hyalomyia ecitonis,* from a series of flies collected by sweeping over a swarm raid of *Eciton foreli* (= *burchelli*) in southern Mexico. Beneway (1961) has examined part of the type series and has based a new genus, *Androeuryops,* on these specimens. *Androeuryops ecitonis* was also found in large numbers over swarm raids of both *burchelli* and *praedator* in Panamá (see table 3). As in some of the species of *Calodexia* discussed below, the proportion of *A. ecitonis* found over *burchelli* was much higher than would be predicted on the basis of the time spent collecting over the two ant species. Of a total of 531 specimens of this species, only two were collected by sweeping where there were no ants. In marked contrast to *Calodexia* in which almost all specimens which were collected over swarms are females, 345 specimens, or about two-thirds of the *Androeuryops* taken, were males.

Although the populations of *Stylogaster* and *Calodexia* remained rather constant from February to August, there was a great change in that of *Androeuryops.* From February through about the first half of May, *Androeuryops* was very abundant, and more than 20 specimens could be collected in 15 minutes over an average-sized swarm of *burchelli.* The maximum abundance was observed on 16 February 1956, when in one hour 216 specimens were taken over a single raid. From 25 May to 18 August the maximum number taken in a 15-minute period was nine specimens. Even when over 100 *Calodexia* were taken, only an occasional *Androeuryops* was found. Therefore, for unknown reasons, *Androeuryops* is abundant in the dry season and early rainy season and then rapidly decreases in abundance. This seasonal fluctuation was so marked that it probably was not unique to 1956. A complete list of the records for *Androeuryops ecitonis* is given below in the "List of Field Numbers with Collecting Data for Flies."

The adults were not seen to hover like *Stylogaster*, and on only two occasions were they seen to fly after cockroaches. In both cases the cockroaches were also being pursued by *Calodexia*. The large number of specimens found from February to May and the constancy of their presence over the swarms, but not near the bivouac, indicate that they are definitely associated with the army ants. Probably they are parasitic on some arthropod flushed out by the ants. The female lays eggs and probably inserts them within the host judging from the large, pointed, and heavily sclerotized ovipositor. Both the egg and ovipositor have been described by Beneway (1961).

THE BEHAVIOR OF CALODEXIA

The tachinid genus *Calodexia* includes 13 species which have been taken on Barro Colorado Island over swarm raids of *Labidus praedator* and/or *Eciton burchelli*. Whereas *Stylogaster* females appear to outnumber the males slightly, 1,783 females but only five males of *Calodexia* were taken over swarms. Curran (1934a: 1-2) also reported that the males "are seldom, if ever, found associated with ants" and "are remarkably rare considering the abundance of females." In his extensive collecting of Diptera on Barro Colorado Island, Curran found males resting on vegetation not near ants and collected 20 specimens, compared with about 150 females taken over ant swarms. I found only one male on vegetation where no ants were seen. Two series of *Calodexia* which were reared included a total of six males and five females, suggesting that the unusual sex ratio near ants is based mainly on a difference in the behavior or survival of the adults.

Like *Stylogaster*, *Calodexia* appears near the bivouac when a swarm raid is starting and stays with the swarm front as it advances. However, *Calodexia* never hovers for more than an instant and normally rests on the low vegetation in the middle of the swarm of ants. *Calodexia* is not as easily frightened away as *Stylogaster* and sweeping over a raid swarm intermittently for an hour does not seem to diminish the number of tachinids. It is also possible to collect them with an aspirator when they are resting near the swarm front.

As the swarm advances farther from the bivouac, the width of the swarm front also normally increases to a maximum of 10 to 15 meters. At the same time the *Calodexia* and *Androeuryops* become more numerous. This is shown by the collection series (1170-1172 and 1411-1415) where sweeping was done in three and five successive timed intervals over two swarms and the flies recorded sepa-

rately for each period. On one day during the first 30 minutes of sweeping (9:45 to 10:45 a. m.) 19 *Calodexia* and 36 *Androeuryops* were taken. During the two following 15-minute periods the numbers of *Calodexia* increased to 22 and 34 and *Androeuryops* increased to 53 and 127. Over the other colony flies were taken in five 15-minute periods starting at 10:00 a. m. The *Calodexia* totals are: 16, 15, 31, 49, and 13. The *Androeuryops* totals are: 7, 14, 37, 32, and 24. The decrease in the number of flies during the last period from 11:00 to 11:15 a. m. is correlated with a decrease in raid intensity as the ants entered the siesta period.

On one occasion a winged cockroach was flushed out by a *burchelli* swarm, and the cockroach was seen to jerk away as three *Calodexia* darted at it as it ran ten centimeters up a small plant. A few seconds later while one fly hovered for an instant over the abdomen of the cockroach, the other two sat on the leaf only three centimeters from the cockroach. The ants then captured the cockroach. Although the *Calodexia* hovered over cockroaches or crickets, they darted at them only when the orthopterans were running or flying. Several *Calodexia* would rest near motionless Orthoptera without making any attempt to attack them until they started to flee. With winged cockroaches the attack in flight may be necessary in order to deposit the larvae directly on the abdomen or under the edges of the terga. However, the flies also waited for wingless cockroaches to move before they would attack. It seems likely that they are able to see most of these cockroaches since the flies hovered directly over them. From the standpoint of survival of *Calodexia* larvae, it would naturally be important to get them on healthy, not injured or dead, hosts. Although the *Calodexia* flew after cockroaches and crickets, they showed little interest in the numerous spiders which ran from the swarm fronts. At times they flew about 30 cm. after a spider but then turned away and rested on a leaf. None of the flies showed any attraction toward amphipods, isopods, phalangids, scorpions, millipeds, centipedes, reduviids, coreiids, pentatomids, cicadas, nor scarabaeids. These are among the more common other arthropods flushed out by the ants, and the number of observations on each of them at the swarm front varies from three to 30 or more.

The species of *Calodexia* all behave similarly with respect to their positions around the ant swarm. They are seldom in the fan area but always can be found throughout the area where the ant swarm is most dense as well as in advance of the front by about two

meters. If in the fan area, they were usually in small groups around or hovering over Orthoptera being attacked by the ants. The only times that the different species appeared to show any species-specific behavior was when an occasional cockroach or cricket ran from the ant swarm. On a few occasions when it was possible to get close enough, it was noticed that flies of only *one* size were pursuing an orthopteran. None of the species of *Calodexia* are distinctive enough to make specific recognition possible in the field. However, since some are more than twice as large as others, on a few occasions it was possible to note that as many as three species were attracted to a single cockroach.

The species of *Calodexia* all rest close to the ground and seem to be found on vegetation more than 50 cm. from the ground only when lower perches are not available. The flies will rest on the ground but apparently prefer slightly elevated perches. They frequently rest on fallen leaves, especially where the edges and tips are curled away from the ground. Ants are continually running up on their perches, and the flies constantly shift, usually avoiding contact with the raiding ants. At times the ants touch a *Calodexia* with their antennae or legs, but no adult fly was ever seen captured, nor were they ever found among thousands of pieces of booty examined. When the flies shift to a new perch to keep up with the swarm or to avoid the ants, they seem to land on any open surface. Then they usually shift position in order to face downward, but they did not seem to show any preference as to whether they faced toward or away from the direction in which the swarm front was moving. At times *Calodexia* is so abundant that there are about ten flies in an area 30 cm. square. In such cases, whenever one fly shifts position a few centimeters, or another one lands nearby, many of the flies in the immediate vicinity fly at least ten centimeters to a new spot.

On every occasion when I have observed the start or end of a *burchelli* or *praedator* swarm raid, the suddenness with which these flies appear or disappear has been impressive. Sweeping throughout an area with a radius of ten meters from a *burchelli* bivouac revealed no *Calodexia,* or at most about ten specimens. Ten to twenty minutes later, when a small swarm raid had advanced only a few square meters, more than 50 *Calodexia* could be found near the swarm front. Apparently they have a good sense of smell and probably spend much time flying through the forest whenever they are not accompanying a swarm. It seems strange

that they were not found more frequently near the bivouac itself. Although the number of flies increases as the swarm front develops during the morning, this increase in numbers is dependent more on the size and intensity of the raid rather than on its duration. The number of flies decreases during the siesta period even though at that time the raid has been in progress for several hours and the ants are spread out over the maximum area. The changes in the number of flies may be dependent upon changes in a "raiding odor" or some stimulating chemical produced by the ants which not only excites the ants, but may also attract the flies. A bivouac of *burchelli* has a much stronger odor than a raid to the human sense of smell, but this may not be true for the flies.

When rain interrupts a swarm raid many of the ants go under leaves, and others return to the bivouac. *Calodexia* also will go under leaves, but a surprising number of them stay on the upper exposed surfaces, and as they get splashed by the rain drops, they wipe the droplets off their bodies with their legs.

When sweeping for flies over the ants, even though no attempt was made to sort the specimens as soon as they were collected, it was immediately evident that several swarms of *L. praedator* had a much higher proportion of the larger species of *Calodexia* than did *burchelli* swarms. Later, when all the specimens had been sorted, distinct differences among the species of *Calodexia* associated with the two species of ants were found, as summarized in table 3. It was estimated that approximately 770 minutes were spent sweeping over swarm raids of *burchelli* and 325 minutes over *praedator* (based on the total time of intermittent sweeping and transferring specimens to killing bottles). Almost all collections were made between 10:00 a. m. and noon when the swarms are largest and the flies most active. A list of the dates and times when these collections were made is given at the end of this paper. These data were analysed by the G-test (Woolf, 1957; Kullback, 1959) to determine if the numbers of flies of each species collected over the two species of ants differed significantly from the proportion expected on the basis of the time spent sweeping over these two species (770:325). The values for G were compared with the Chi-square distribution which closely approximates that for G. It is interesting that these comparisons all show either no significant difference from what might be expected based on the total collecting times, or else they are highly significant, with no borderline cases. It is clear that six of the 12 species tested show a preference for one or the other ant

TABLE 3.—Summary of Collection Records for Tachinidae

Species of *Calodexia* or *Androeuryops*	Number and percent over *Eciton burchelli* swarm raids		Number and percent over *Labidus praedator* swarm raids		Total over both species	G–test
C. agilis	194	69%	87	31%	281	0.21 n. s.
C. apicalis	0	0	2	100	2	.....
C. bella	50	91	5	9	55	13.85†
C. continua	85	71	34	29	119	0.07 n. s.
C. dives	60	30	137	70	197	132.89†
C. fasciata	190	78	53	22	243	7.65†
C. fumosa	24	28	61	72	85	63.92†
C. interrupta	105	65	56	35	161	1.95 n. s.
C. major	29	64	16	36	45	0.72 n. s.
C. panamensis	2	7	27	93	29	52.45†
C. similis	77	73	28	27	105	0.46 n. s.
C. varia	4	44	5	56	9	2.60 n. s.
C. venteris	345	79	89	21	434	18.79†
Calodexia total	1165	66	600	34	1765	14.77†
A. ecitonis	483	91	46	9	529	138.82†

† P = < 0.001 n. s. = not significant.

species, and in two cases, *dives* and *panamensis* this is especially marked.

The biological significance of these results is doubtful. It is possible that some species of *Calodexia* are attracted to one species of ant more than to the other on the basis of the odor differences of the ants with no survival advantages for the fly. However, for certain species of *Calodexia,* there may be an advantage attributable to the different raiding behavior of the ants. The more subterranean *Labidus praedator* clearly raids to a larger degree under leaves and other objects which are close to the ground. Because of this difference in raiding, it is probable that *praedator* drives out some species of arthropods which are not often disturbed by *burchelli.* The workers of *praedator* are smaller than those of *burchelli,* and the former appear to capture more smaller arthropods while perhaps missing more of the larger orthopterans. In addition, *burchelli* raids more frequently and much higher up trees, going near the tops of the tallest trees more than 30 meters from the ground. It is not known whether any of the flies follow the swarm raids in these trees, but this arboreal raiding must drive out many arthropods not found on the forest floor. Other than the gross behavior of the ants, there is no evidence for a difference in the proportions of potential hosts driven out, since no quantitative nor qualitative study of the arthropods either driven out or eaten by the ants has been made. Knowledge of the hosts may eventually support the observed differences in the proportions of the different *Calodexia* species associated with the two species of army ants. However, at this time no reliable conclusion can be reached because far too few hosts are known.

In addition to *Calodexia* associated with *burchelli* and *praedator,* two specimens were found near the unusual swarm raid of *Eciton vagans* (discussed earlier, under *Stylogaster*). After the bivouac of this colony was located, and the queen, a large sample of the workers, and part of the sexual brood were taken, it was discovered that *Calodexia* had been attracted to the ants milling around the bivouac site. About 50 flies were in the area and 18 were taken. In contrast to this experience with a disturbed bivouac of *vagans,* no *Calodexia* could be found near the ants milling around more than 20 nests of *E. hamatum* which had been similarly disturbed. As with all other species of *Eciton,* the odor from a bivouac of *E. hamatum* becomes much stronger when the ants are disturbed.

The Life Cycle of Calodexia

Although *Calodexia* is much more numerous around the swarm front than *Stylogaster*, there are fewer records of its presence and less speculation about its biology. This is probably due to the unusual morphology of *Stylogaster* and the fact that the Tachinidae are poorly known taxonomically. *Calodexia* is not conspicuously different from hundreds of other genera of higher Diptera, and very little work has been done on the taxonomy of the genus even though it is widely distributed from Mexico to Brazil (and probably Argentina). The most extensive previous collection was made by Curran, who has also described most of the species of *Calodexia*. He gave only brief comments on their association with army ants and decided that the flies parasitized cockroaches since they flew after them (Curran, 1934a: 1-2). Curran did not know whether *Calodexia* deposited eggs or larvae and did not identify any of the ants or cockroaches involved. The only positive information on their life cycle was given by Lopes (1937: 260) who reared "*Calodexia ?venteris*" from one specimen of *Periplaneta americana*, apparently taken as it was escaping from a swarm raid of *Labidus praedator*.

All females of *Calodexia* which were examined had more than 25 larvae in their oviducts, and some had over 200 arranged in dense, continuous spirals, showing progressive development from small eggs to actively squirming larvae. It is very easy to slit the membrane between the first and second abdominal segments and remove the posterior segments from either a dried or fresh specimen. Dried abdomens then can be softened in hot water or Nesbitt's clearing solution and the oviducts and larvae removed. Larvae from dried specimens are readily expanded and cleared in Nesbitt's solution and can be mounted directly on slides in Hoyer's medium. (See the section on "The Life Cycle of *Stylogaster*" for formulas of these solutions.) First instar larvae of eight species were examined; these all showed specific characters.

The first instar larvae have an indistinct pseudocephalon which lacks spines and shows no clear separation from the first thoracic segment. (The terminology for the larvae used here follows that of Roback [1951].) The three thoracic segments have very fine spinules in segmental bands and some species have ventral patches of strong spines on the meso- and metathoracic segments. All first instar larvae examined have strong bands of abdominal spines.

These bands are composed of about five rows of spines of varying lengths and shapes, arranged so that the spines are contiguous for most of the width of the larva. The arrangement and shape of these spines are useful for separating species. There are hooks at the posterior end of the body near the simple posterior spiracles, and these hooks probably are used to hold on to part of host's tracheal system. The buccal armature is thin and long with broad or long, thin, sharp hooks. These larvae appear well-adapted for piercing a host and for moving on most surfaces. Females dropped larvae when they were etherized, killed in cyanide bottles, or if their abdomens were squeezed. These larvae were very active when they came out of the female. Probably they are dropped on the surface of the host and then burrow into it, since the larvipositor of the female shows no piercing adaptations. Although all instars have excellent specific characters among the few species where more than the first instar is known, there do not seem to be any specific characters which are stable throughout the larval period. Therefore, it is impossible to identify later instars by comparison with the larvae removed from adult flies.

The second instars lose the prominent bands of spines but retain bands of spinules or roughened areas. The oral hooks become much broader and very different in shape, prothoracic spiracles develop, and there is a prominent papilla (antenna?) at each anterolateral angle of the pseudocephalon. The third instar larva has a pair of large posterior spiracular plates with peritremes which are almost closed. A button and three elongate, almost straight, spiracular slits are found on each plate. The oral hooks are shorter and broader than in the second instar, and there are two small holes in the central area of the basal part of each hook. The ventral edges of the hooks may have a series of fine teeth.

Only one series of *Calodexia* was reared to adults from a determined host parasitized in the forest under natural conditions. This series of eight *C. interrupta* was reared from a gryllid, *Ponca venosa* Hebard (2260-X), which was taken as it was running from a swarm raid of *burchelli*. Three to five adults of *Calodexia* were seen to fly closely after the cricket as it ran about a meter in advance of the ants. This cricket was taken on 7 August 1956, and on 11 August nine puparia were found in the rearing vial. Four males emerged on 21 August and four females on 22 August. No fly emerged from the ninth puparium, and no additional larvae could be found in the cricket. Thus, the larval stage was very short, with a duration

of about four days; and the pupal stage lasted 10 to 11 days. No larvae were found in four additional specimens of *Ponca venosa* (2231, 2157) which were dissected 4, 6, 16, and 28 days after groups of *Calodexia* were seen flying after them in front of raid swarms.

In addition to this one case where the species of both host and parasite are known, there are several less complete cases. One *Calodexia* pupa was reared from a cockroach (2259) taken on 1 August as it was running while pursued by *L. praedator* and *Calodexia.* The cockroach died on 5 August, and the single puparium was found on 6 August, but no adult emerged. The oral hooks from this puparium are very similar to those from a known *C. venteris* puparium, but positive identification cannot be made until other puparia are available.

A gryllid, *Eneoptera* sp. (2205), taken as it was running away from a swarm raid of *Labidus praedator* on 27 July, was dissected on the same day. Three first instar *Calodexia* larvae near *agilis* or *interrupta* were found inside near the dorsum of the first abdominal segment. These larvae were not firmly imbedded nor attached to any tissue, but they may have shifted in position after the cricket was killed. A second *Eneoptera* sp. (2184) taken under similar conditions was dissected 60 hours after the time of suspected larviposition. Three small second instar larvae and nine early third instars, perhaps of the same species, were found in it. In a third specimen of *Eneoptera* (2231) taken in similar circumstances no larvae could be found.

Two cockroaches, *Epilampra azteca* Saussure (2069-A, 2069-B), were taken escaping from a *praedator* swarm on 5 July. One was dissected that day and no larvae were found in it. The second specimen was dissected 24 hours after the time of suspected larviposition, and nine larvae were found in it. All these appear to be second instar *Calodexia* larvae. These larvae were found close to the abdominal body wall of the cockroach except for one or two which were either close to the gut or were pulled away from the body wall when the cockroach was dissected. A subsequent attempt to introduce *Calodexia* larvae into a specimen of *Epilampra azteca* (2295) was unsuccessful and when it was dissected after eight days, no larvae could be found.

A cockroach nymph (2069-C) which could not be identified to genus was taken at the same time as the above mentioned *Epilampra.* When it was running from the ants, it was clearly seen to be pursued by several females of one of the largest species of *Calodexia*

and by no other flies. A puparium was found on 15 August in the rearing vial with this cockroach, but the larva probably came out of the cockroach several days earlier. No adult emerged from this puparium. In December, 1959, the puparium was dissected and an advanced, but light-colored, female pupa of *Calodexia dives* was found in it. In spite of the incomplete development this specimen could be determined since it is the only *Calodexia* which lacks presutural acrosticals and has one pair of postsutural acrosticals. Although other species of *Calodexia* were flying nearby, it is noteworthy that only large *Calodexia* were seen to pursue these last three cockroaches. However, the nymph in which the *dives* developed was a small host, only about 15 mm. long. On one occasion a single *C. dives* was taken as it and at least two other smaller species hovered over a cricket (*?Ponca venosa*) being attacked by the ants.

About 12 larvae from *Calodexia venteris* were introduced into each of two specimens of *Eublaberus posticus* (Erickson) (2235, 2236) on 30 July 1956. On 5 August four puparia and one mature larva were found outside of the second cockroach, and two males and one female *C. venteris* emerged from these puparia on 18 August. Although the cockroach appeared weak, it remained alive until 6 August. It was not preserved in alcohol until 18 August, however, since additional larvae were still seen inside it. When the cockroach was dissected, four first or second instar larvae were found which were probably laid on the cockroach after it died. Nine second instar larvae, which might be *Calodexia,* and the three larger second instar larvae, which were discussed above as possible *Stylogaster,* were also found.

In hopes of rearing specimens of males, which are almost impossible to find near the ant swarms, *Calodexia* larvae were introduced into additional insects which were readily available at the laboratory. The following insects were tried: prepupae and pupae of *Polistes* and a sphecid mud dauber, tettigoniids (*Chloroscirtus discocercus* Rehn, *Euceraia* sp., *Microcentrum stylatum* Hebard, *M. philammon* Rehn, *Microcentrum* sp., and *Phylloptera dimidiata* Brunner), gryllids (undetermined nymphs), and cockroaches (*Eurycotis* sp., *Periplaneta brunnea* [Burm.], and undetermined nymphs). No larvae completed development in any of these "hosts," although in a few cases they were seen moving under the body wall for at least a day following the insertion of the larvae. Several first instars at least doubled in size, and two *C. fumosa*

larvae (2242-C) developed to second instars in a tettigoniid which died a few hours after they were inserted.

In summary, the known fragments concerning the behavior and biology of *Calodexia* indicate that the different species are all larviparous and internal parasites of Blattoidea and Gryllidae. The larval period is only four or five days and the pupal stage lasts ten or 11 days. These were reared under fluctuating laboratory conditions at around 28° C. which is slightly warmer than forest floor temperatures. Even allowing for the possibility that some first instar larvae were overlooked in dissecting the hosts, it is clear that of the cockroaches and crickets which escape the ants, 50% to 90% are subsequently parasitized by the flies accompanying the ants. In most cases this parasitism is fatal to the host.

OBSERVATIONS ON THE TAXONOMY OF CALODEXIA

All 23 known species of *Calodexia* are included below in a table of diagnostic characters and a key. Additional records and clarifications of the original descriptions are also given for all species found on Barro Colorado Island. Nine species in the genus have not been examined by the author, and the brief treatment of them is abstracted from the published descriptions. About 170 specimens, representing thirteen species, were previously known from Barro Colorado Island. Since most of these species were based on few individuals, examination of 1802 additional specimens from this locality has revealed a few errors and more variation than reported in the original descriptions. Possible geographical variation is not involved here because all the specimens are from the type locality except for the specimens of *similis* and *fumosa*.

In the generic and specific diagnoses given below, all characters which are not mentioned are considered to agree with the original descriptions. *Only* additions or major modifications of the descriptions are included. Information on specific characters which can be easily presented in table 4 is not repeated in the comments for each species unless some clarification seems desirable.

Throughout the present treatment the terms used by Curran (1934a, 1934b) have been used, but in some cases modifications of these terms have been made in an attempt to be more precise. The method of describing the arrangement of bristles follows that used by many dipterists, *e. g.*, acrosticals 1-3 means that there is one pair of presutural and three pairs of postsutural acrostical bristles. The term frontals is used for the row of bristles along the inner edge of the parafrontals and includes both the proclinate

and reclinate orbital bristles. The width of the eye is measured perpendicularly to the median margin of the eye when the head is observed perpendicularly to the anterior surface. Abdominal terga are numbered as in Curran, *i. e.*, the "first tergum" is the first obvious segment, but morphologically, it is the second tergum. Other terms are explained here with reference to table 4, and the abbreviations used in that table are given in parentheses. A question mark (?) indicates that the state of a character cannot be determined with certainty from the published description. Where several states are included for the same character, the most common state is italicized; *e. g.*, number of bristles 2-3. This indicates most specimens have two bristles, but an occasional fly or possibly as many as ten percent of the specimens have three bristles. Where fractions are used, *e. g.*, ½ (abbreviated as 1), ⅔ (2), the abbreviation 1-2 means from ½ to ⅔. For all thoracic and abdominal characters using patterns of pollen or vittae, the specimens should be viewed with the light striking the specimen at a slightly posterior angle. Small bristles have been included in the counts of bristles when they are only slightly larger than neighboring hairs and in the "correct positions." When looking perpendicularly at a section of body wall using a microscope with a bright light and 40 × magnification, "white" hairs usually cannot be seen although they can be seen when the specimen is turned more obliquely to the line of sight. "Black" hairs can be seen in perpendicular view as well as in oblique view and are usually shorter and coarser than white hairs. "Black" hairs in some lights have a brownish or reddish sheen.

Throughout this paper the following colors are referred to only by the primary color: orange, usually a dull, pale, slightly brownish-orange (o); yellow, a dull, pale straw color or slightly brownish yellow (y); gold (g); brown (br); black, due to pollen often appears brownish in some lights (b); bluish (bl); white to pale gray-white (w). Combinations of these symbols are also used; *e. g.*, (obr) = orange-brown; (o-br) = orange to brown (where color varies from orange to brown in a single specimen or species). All observations were made with a stereoscopic microscope using 40 × magnification and a fairly bright light (Spencer microscope light). Under lower magnification and dimmer light the colors look darker and closer to the colors as given in Curran (1934a).

Notes applicable only to an individual character are given below and are numbered to correspond to the numbers in the left-hand column of table 4.

1. Color of occipital pollen: Mostly white to yellowish on posterior aspect of head, but dorsal and median black bands of pollen may be present (w); mostly black, but lateral edges may be whitish (b). Specimens should be examined laterally to see maximum amount of white pollen.
2. Downward extent of row of black bristles along outer edge of occiput measured as fraction of length of eye: Fractions ½, ⅔, ¾, and ¼ (extending completely under eye) are abbreviated as 1, 2, 3, and 4. Head is observed laterally to determine length of eye and extent of occipital bristles.
3. Width of palp: Nearly equal throughout its length or enlarged apically to about twice the width of the basal half (e); greatly enlarged near apex to three or four times width of basal half (en).
7. Anterior outer dark vittae of mesothorax: Do not extend anteriorly to reach the position of median sublaterals (ne); extend to level of median sublaterals (es); extend anteriorly beyond position of median sublaterals (ea). Where outer dark vittae are greatly narrowed but continue as fine lines to anterior surface of thorax, only broad main vittae are considered. Where there is a darker stripe in the middle of an area lacking white pollen, the entire dark area is considered to be the vitta, not only the darker stripe.
8. Median postsutural dark vittae of mesothorax: United for approximately their entire lengths to form a single board vitta, but median section of this vitta may be more grey or have a few light pollen spots (u); separated directly behind suture by light pollen but joined posteriorly for about one-half their lengths (sbs); separated for entire lengths behind suture (sel).
9. Light colored postsutural mesothoracic vittae which separate outer dark vittae from median dark vittae: Absent, so that all postsutural dark vittae are united for at least half their lengths, usually appearing as wide solid black fascia across thorax behind suture (a); narrow, at widest point about half width of an outer dark vittae (n); about equal in width to an outer black vittae (e).
11. Marginal scutellar bristles include lateral bristles and large pair on posterior lateral angles of scutellum but not apical marginals. (Townsend [1912: 309] includes posterior lateral marginals with apicals.)
14. Infrasquamal cilia are sometimes reduced or absent.
20. Posterior femora when seen ventrally: Only proximal one-third to three-fourth orange (po); or color of entire ventral surface except distal extremity (o, br, etc.). Specimens should be turned to view posterior femora from several angles to see maximum amount of light color in ventral view.
21. Ventral yellow cilia are arranged in more distinct rows than majority of hairs on ventral surface of femur, and longest cilia are at least as long as thickness of tibia. Few scattered hairs on inner or outer central margins not considered to be rows unless they extend along at least half length of femur.
22. Color of shining dorsal abdominal pollen (ignoring duller gray-white pollen). Specimens examined with light striking dorsal surface approxi-

mately perpendicularly to give brightest and most highly colored reflection from pollen.

23. Color of dorsum of first tergum (ignoring pollen): Orange, may have a weak middorsal dark stripe (o); orange with strong middorsal dark stripe about as wide as distance between marginals (os); entirely brown (br); or black, usually with brown pollen (b).

24. Whitish pollen on dorsum of first abdominal tergum: Abundant and dense at any point in dorsal view (dwp); absent or sparse (a).

25. Light pollen of ventral areas of both first and second abdominal terga: Equally white and dense (e); absent or much less white and less dense on first compared with second tergum (a); absent or weak on venters of both terga (aa).

26. Pale pollen on second abdominal tergum: Not interrupted by median longitudinal stripe (ni); interrupted for almost entire length of tergum by narrow dark or pollenless median stripe less than half as wide as distance between distals (ns); interrupted by wide, dark or pollenless stripe at least as broad as distance between distals (ws). Specimens should be observed in posterior dorsal view to show maximum extent of pale pollen.

28. Lateral marginals are same as "lateral bristles" of some authors. Ventral marginals include bristles on tergum ventral to laterals.

29. Pale pollen on third abdominal tergum: Extending posteriorly to margin between median marginals (ex); not extending posteriorly between median marginals, but small marginal spot not connected with pale basal fascia may be present (ne).

32. Dark fascia on 4th tergum: Absent (a); or extending basally from median apical margin of the tergum ½, ⅔, ¾, or ¼ distance to basal margin (abbreviated 1, 2, 3, 4 respectively). The entire surface of tergum should be observed from behind to determine maximum contrast between white pollen and dark fascia.

34. Body length is measured from anterior surface of third antennal segment (when it is in normal position close against surface of head) to most posterior part of abdomen (not to end of larvipositor or most posterior part of abdomen in a morphological sense).

36. Total number of specimens and number of types examined by present author are listed in detail under discussions of each species. The number of specimens is given in parentheses and refers to females unless males are indicated. All specimens were taken on Barro Colorado Island, and details concerning their collection are given in a list of all field numbers at the end of the species discussions.

TABLE 4.—Diagnostic Characters for Known Species of Calodexia

CHARACTERS	*continua*	*interrupta*		*dives*	*caudata*	*similis*		*agilis*	*varia*	*mexicana*
	♀	♀	♂	♀	♂	♀	♂	♀	♀	♀
1. Color of occipital pollen: white to yellowish (w); black (b)	w	w	w	w	w	w	w	w	w	w
2. Downward extent of black occipital bristles: *1/2*; *2/3*; *3/4*; *4/4*	1–*2*	2	2	2	2–3?	1–2	3	2–*3*	4	?
3. Width of palp: about equal (e); greatly enlarged near apex (en)	e	e	e	e	e?	e	en	e	e	?
4. Color of third antennal segment distal to the insertion of the arista	o–obr	o–obr	o–obr	o–br	o?	o–br	br–b	*o*–obr	o–*br*	br
5. Number of pairs of presutural acrosticals	1	1	1	0	1	*1*–2	1	1	1	2
6. Number of pairs of postsutural acrosticals	1	1	1	1	1	*1*–2	1	1	3	3
7. Anterior extent of outer dark vittae compared with median sublaterals	ea	ea	ea	ea	?	ea	ea	ea	ea	?
8. Median dark vittae behind suture: united; separated by light pollen	u	u	u	u	u	u	u	u	sel	?
9. Outer postsutural light vittae: absent (a); narrow (n); equal (e)	n	n–*e*	n–*e*	n	n–e?	n	n	n–e	n	?
10. Dorsum of scutellum: white; black; white with basal black band (bb)	bb	bb	bb	bb	bb?	bb	bb	bb	w	bb?
11. Number of pairs of lateral marginal scutellar bristles	3	3	3	2–*3*	3	3	3	*3*–4	3	3
12. Color of pile on sternopleura and lower anterior mesopleura	w	w–*y*	w–*y*	w	w	w	w	b	b	?
13. Notopleural hair: absent (a); color when present (b, w, y)	w	a–*b*	b	b	w	w–y–*b*	w–y	b	b	?
14. Infrasquamal cilia: black or occasionally absent (b); yellow (y)	b	b	b	b	b	b	b	b	b	?
15. Color of anterior surface of front coxae (ignoring pollen)	o–br	o–*br*	o–br	o–br	o–br?	o–br	o–br	o–obr	o–*br*	?
16. Color of hairs on front coxae (not including bristles)	w	*b*+w	*b*+w	w	w, b?	w	w	b	b	?
17. Total number of black hairs and bristles on one front coxa	10–18	20–50	20–50	9–15	?	5–10	25–35	40–55	50+	?
18. Number of ventral bristles near middle of middle tibia	1–*2*	1	1	1	1	1	1	1	1	?
19. Number of anterior bristles near middle of middle femur	2	2	2	2	1	2	2	*2*–3	2	2
20. Ventral color of posterior femora: proximally orange (po); entire color	br	br–b	br–b	o–br?	br	po	po	*po*–o	b	?
21. Number of rows of ventral yellow cilia on posterior femur	0	0	1	0	1	0	0	0	0	0?
22. Color of dorsal abdominal pollen	y	y	y–*g*	bl	?	w–y	w–y	bl–y	bl	?
23. Color of dorsum of first tergum and stripe (s) if present	b	b	ybr–b	b	os	b	b	b	b	br
24. Dorsal white pollen on first tergum: dense (dwp); absent or weak (a)	*a*–dwp	a	a	a	a?	a	a	a	dwp	?
25. Ventral pollen on first tergum: absent; equal to second; absent on both	e	*a*–e	a	e	?	e	a–e	a	a–e	?
26. Pollen on second tergum: interrupted by narrow or wide stripe or none	ni	ni	ni	ni–ns	?	ni	ns	ni–*ns*	ni	?
27. Median marginals on second tergum: number of pairs; or a row	1	1	1	1	1	1	1	1	1	?
28. Number of pairs of lateral and ventral marginals on second tergum	1	1	1	1	1?	*1*–2+	1	1	*1*–2+	?
29. Pollen of third tergum: extended; not extended to median margin	ne	ex	ne–ex	ex–ne	?	ex	ex	ex	ex	?
30. Number of discals on third tergum	2	2	2	2	2	2	2	2	*2*–9	4
31. Color of central area of fourth tergum (ignoring pollen)	*o*–br	o–*br*	o–b	br–b	br?	b	br–b	obr–b	br–*b*	o?
32. Dark fascia on fourth tergum extending basad: *1/2*; *2/3*; *3/4*; *4/4*; absent	1–3	1	1	a	1–2?	a–*1*–2	1	a–*1*–2	a	?
33. Discals on fourth tergum: number; or row of unknown number	8–10	8–12	7–8	6–12	5+	9–17	4–6	6–10	6–14	?
34. Minimum body length in millimeters or length of single specimen	5.7	4.8	7.5	6.0	11.0?	5.9	6.1	5.5	6.3	6.5
35. Maximum body length in millimeters	8.0	7.2	7.7	9.0	.....	8.3	7.0	8.2	7.8	.....
36. Number of specimens examined	122	173	3	197	0	105	2	286	10	0

TABLE 4.—Diagnostic Characters for Known Species of Calodexia—*Continued*

CHARACTERS	*bella*		*bequaerti*	*panamensis*		*valera*	*fumosa*	*aldrichi*	*townsendi*	*fulvibasis*
	♀	♂	♀	♀	♂	♂	♀	♀	♀	♀
1. Color of occipital pollen: white to yellowish (w); black (b)	w	w	w	w	w	w	b	b	w	w
2. Downward extent of black occipital bristles: *1/2*; *2/3*; *3/4*; *4/4*	1–*2*	2	4	4	4	4	4	3?	4	2–3?
3. Width of palp: about equal (e); greatly enlarged near apex (en)	e	e	e	e	e?	e?	e	e?	e?	e?
4. Color of third antennal segment distal to the insertion of the arista	o–*br*	o–*br*	br	o–br	o–*br*	o–*br*	o–*br*	br?	b?	br?
5. Number of pairs of presutural acrosticals	1–2	*2*	2	*2*–3	2	3	2–*3*	1	0	0
6. Number of pairs of postsutural acrosticals	*1*–2	1	3	3	3	3	1	1	0	0
7. Anterior extent of outer dark vittae compared with median sublaterals	ne	ne	ea	ea	?	?	ea	ea	ne?	?
8. Median dark vittae behind suture: united; separated by light pollen	u	u	u	u	u	u	u	u	u	sel
9. Outer postsutural light vittae: absent (a); narrow (n); equal (e)	a	a	n	n–e	n–e?	a	a	a?	a?–u?	n–e?
10. Dorsum of scutellum: white; black; white with basal black band (bb)	bb	bb	bb	bb	bb	bb	b	b	b?	bb?
11. Number of pairs of lateral marginal scutellar bristles	2	*2*–3	3	3	3	3?	2–*3*	3	3	3
12. Color of pile on sternopleura and lower anterior mesopleura	b	b	b	b	b	b	b	b	b	b
13. Notopleural hair: absent (a); color when present (b, w, y)	*a*–b	*a*–b	b	b	b	b	*a*–b	a?–b?	b	b
14. Infrasquamal cilia: black or occasionally absent (b); yellow (y)	b	b	b	b	b	b?	b	b?	b?	b?
15. Color of anterior surface of front coxae (ignoring pollen)	br	br	br	o–*br*	?	?	y*br*	br?	b	?
16. Color of hairs on front coxae (not including bristles)	b	b	b	b	b	b	b	b?	b	b?
17. Total number of black hairs and bristles on one front coxa	35–45	35–45	25–35	25–35	?	?	15–25	?	?	?
18. Number of ventral bristles near middle of middle tibia	1	1	1	1	1	1	0	0	1	1
19. Number of anterior bristles near middle of middle femur	2	1	2	2	?	?	*1*–2	?	1	?
20. Ventral color of posterior femora: proximally orange (po); entire color	br	br	br	br	br	b?	y*br*	?	b	po
21. Number of rows of ventral yellow cilia on posterior femur	0	0	0	0	?	?	0	0	?	?
22. Color of dorsal abdominal pollen	w	y–g	w	w–y	y?	w?	w–bl	?	bl?	w?
23. Color of dorsum of first tergum and stripe (s) if present	b	y–*br*	b	b	y–br	br	br–b	br–b?	b	b
24. Dorsal white pollen on first tergum: dense (dwp); absent or weak (a)	a	a	a	a	a?	a?	a	a?	a?	a?
25. Ventral pollen on first tergum: absent; equal to second; absent on both	a	a	a	a	a?	a?	a	?	a?	a?
26. Pollen on second tergum: interrupted by narrow or wide stripe or none	ni	ni–ns	ni	ni	?	?	ws	?	?	ns–ws
27. Median marginals on second tergum: number of pairs; or a row	1	1	1	1	1	1	1	row	1	1
28. Number of pairs of lateral and ventral marginals on second tergum	1	1	1	*1*–2	?	?	1–*2*+	?	?	?
29. Pollen of third tergum: extended; not extended to median margin	ne	ne	*ne*–ex	ne–ex	?	?	ne	ne	?	?
30. Number of discals on third tergum	2	2	2	2	2	2	2	2	2	2
31. Color of central area of fourth tergum (ignoring pollen)	b	o–brb	br	*br*–b	?	?	obr	?	br?	br?
32. Dark fascia on fourth tergum extending basad: *1/2*; *2/3*; *3/4*; *4/4*; absent	4	4	a	a	1	2	4	4	1–3?	1–3?
33. Discals on fourth tergum: number; or row of unknown number	4–*6*–8	2–7	9–12	8–14	row	row	4–10	5+	6	4
34. Minimum body length in millimeters or length of single specimen	4.0	5.3	4.5	4.1	4.5	8.0	3.1	5.2	6.0	6.0
35. Maximum body length in millimeters	6.4	6.8	.....	6.1	7.0	.....	4.5	.....	.....	.....
36. Number of specimens examined	56	4	1	29	0	0	84	0	0	0

TABLE 4.—Diagnostic Characters for Known Species of Calodexia—*Concluded*

CHARACTERS	*major*		*flavipes*	*majuscula*	*venteris*		*insolita*	*apicalis*		*fasciata*
	♀	♂	♂	♂	♀	♂	♀	♀	♂	♀
1. Color of occipital pollen: white to yellowish (w); black (b)	w	w	w	w	w	w	w	w	w	w
2. Downward extent of black occipital bristles: *1/2*; *2/3*; *3/4*; *4/4*	2	2	?	?	*1–2*	*1–2*	3	1–2	1–2	*2–3*
3. Width of palp: about equal (e); greatly enlarged near apex (en)	e	e	?	e	e	e	e?	e	e?	e
4. Color of third antennal segment distal to the insertion of the arista	*o*–obr	*o*–obr	br?	o-br	*y*–obr	o	o	yo	yo?	o–br
5. Number of pairs of presutural acrosticals	1	1	1	1?	1	1	1	1	1	*1–2–3*
6. Number of pairs of postsutural acrosticals	1	1	1	1	1	1	1	1	1	*1–2*
7. Anterior extent of outer dark vittae compared with median sublaterals	ea	ea	?	?	ea	ea	?	ne	ne?	ne
8. Median dark vittae behind suture: united; separated by light pollen	sbs	sbs	u?	?	u	u	u	u	u	u
9. Outer postsutural light vittae: absent (a); narrow (n); equal (e)	u	n–*e*	n–e	e	a–n	n	n	a	a	*a*–n
10. Dorsum of scutellum: white; black; white with basal black band (bb)	bb	bb	b?	bb?	bb	bb	bb	bb	bb	bb
11. Number of pairs of lateral marginal scutellar bristles	3	3	3	?	3	2–3	3	2	2	2
12. Color of pile on sternopleura and lower anterior mesopleura	w–y	w–y	?	?	w–y	w–y	b	b	b	b
13. Notopleural hair: absent (a); color when present (b, w, y)	b	b	?	?	a–w–b	a–w–y	?	b	b?	a–*b*
14. Infrasquamal cilia: black or occasionally absent (b); yellow (y)	b	b	b	w–y	b	b	b	b	b	b
15. Color of anterior surface of front coxae (ignoring pollen)	*o*–obr	o	o?	y? o?	y–o	y	o?	*o*–obr	o?	*o*–br
16. Color of hairs on front coxae (not including bristles)	w–*y–b*	w–*y–b*	?	?	w–*y–b*	w–*y*	?	b	?	b
17. Total number of black hairs and bristles on one front coxa	25–50	20–30	?	?	5–30	5–10	?	35–55	?	25–35
18. Number of ventral bristles near middle of middle tibia	1	1	1	1	1	1	1	1	1	0
19. Number of anterior bristles near middle of middle femur	2	2	?	?	2	1	?	2	2?	2
20. Ventral color of posterior femora: proximally orange (po); entire color	po	po	po	o	*o*–ybr	y–ybr	po–o?	po	po	po
21. Number of rows of ventral yellow cilia on posterior femur	0	1	2	1, 2?	0	1	0	0	0	0
22. Color of dorsal abdominal pollen	bl	w–y	?	?	y–g	g	?	bl	?	w–y
23. Color of dorsum of first tergum and stripe (s) if present	b	o–*os*	os	ys	os	o	?	b	b	br–b
24. Dorsal white pollen on first tergum: dense (dwp); absent or weak (a)	a	a	a?	?	a	a	?	a	a	a
25. Ventral pollen on first tergum: absent; equal to second; absent on both	a	a	?	?	a	aa	?	a	a?	a
26. Pollen on second tergum: interrupted by narrow or wide stripe or none	ns	ns	?	?	*ni*–ns	ni	?	ni–ns	?	*ni*–ws
27. Median marginals on second tergum: number of pairs; or a row	1	1	1	1	1	1	1	1	1	1
28. Number of pairs of lateral and ventral marginals on second tergum	1	1	?	1?	1	1	?	1	1?	1–*2*+
29. Pollen of third tergum: extended; not extended to median margin	ex	*ex* ne	?	?	*ne*–ex	ne	?	ne	?	ne
30. Number of discals on third tergum	2	2	2	2	2	2	2	2	2	2
31. Color of central area of fourth tergum (ignoring pollen)	*br*–b	o–brb	?	?	obr–b	o	?	br–b	br–b	o–b
32. Dark fascia on fourth tergum extending basad: *1/2*; *2/3*; *3/4*; *4/4*; absent	a–1–2	1–3	?	?	*1–3*	1	?	4	4	1–3
33. Discals on fourth tergum: number: or row of unknown number	5–11	6–7	row	row	6–10	6	4	*2–4*	2	7–14
34. Minimum body length in millimeters or length of single specimen	6.8	8.8	9.6	10.0	5.3	8.2	7.5	6.9	8.0	4.0
35. Maximum body length in millimeters	8.9	9.2	.....	.....	8.6	8.3	.....	7.5	8.5	6.7
36. Number of specimens examined	43	2	0	0	441	2	0	2	0	244

CALODEXIA VAN DER WULP

Calodexia van der Wulp (1891:257). Brauer and Bergenstamm (1891:375-376, 1893:130-131), diagnosis. Coquillett (1910:517), *C. majuscula* designated as type species. Townsend (1927:219), key. Curran (1934a:2-3), diagnosis. Curran (in Curran, et al. 1934:505-506), diagnosis. Curran (1934b:432, 439, 461), key, figures of head, wing.

Oestrogaster Townsend (1912:310; 1914:28). Townsend (1927:223), key. Aldrich (1929:21).

Oestrogastropsis Townsend (1915:424). Townsend (1927:223), key. Aldrich (1929:21).

Oestrogastrodes Townsend (1915:425). Townsend (1927:225), key. Aldrich (1929:21).

The generic diagnosis given by Curran (1934a: 2-3) is considered to be correct except for the following modifications.

Occiput with white or yellowish pile and black, white, or yellowish pollen; row of black occipital bristles extends downward at least half length of eye. Check at narrowest point 1/7th to 1/5th as wide as height of eye (= maximum length of eye); ocellars short and weak; outer verticals present in females, may be absent in males; palpus with parallel sides or slightly enlarged at apex and with rounded or bluntly pointed tip, some males with apex of palpus swollen to form ovoid club; prementum about twice as long as wide in lateral view. Dorsocentrals 2-3, rarely 3-3; acrosticals usually 1-1, sometimes 0-0, 0-1, 1-3, 2-1, 2-3, 3-1, 3-3, rarely 0-2, 1-2, 2-1, or 2-2, one or more pairs often weak; no presutural intra-alar (= posterior sublateral); anterior intra-alar often weak but rarely absent; presutural present. Middle of propleuron bare; mesopleuron and sternopleuron with fine white, yellowish, or coarser black hairs. Scutellum with two to four pairs of marginals; first pair strong; last pair, located on posterior lateral angle of scutellum, also strong; intermediate pair(s) weak or absent; in addition, a weak or strong apical pair or rarely two weak apical pairs may be present; pollen of scutellum usually dark basally, light at apex, but sometimes entirely light or dark. Squama white, often with faint brown or pale yellow-brown tinge in center or on most of posterior lobe; infrasquamal setulae usually present and black, sometimes absent or yellow. Middle femur with two, occasionally one or three, anterior bristles near middle. Males often with dense row of yellow hairs along inner ventral margin of hind femur, sometimes with rows on both inner and outer margins or no distinct row. Middle tibia usually with one ventral bristle near middle, sometimes a second shorter bristle or no ventral bristle near middle; anterior tibia with one posterior bristle near middle. Abdomen

black, often partially yellow, orange, or reddish and with pale pollen; second and third terga of most species each with basal band of whitish pollen which widens medially; first and second abdominal terga each with a pair of median marginals and a pair of lateral marginals, sometimes with weak row of lateral marginals; third tergum usually with one pair of discals, occasionally one row of four or more; fourth tergum without discals or with one or two rows or a pair.

KEY TO SPECIES OF CALODEXIA

Modified from that in Curran (1934a: 3-4)

1. Occipital pollen mostly black 2
   Occipital pollen mostly white or yellowish 3

2 (1). Acrosticals 3-1 or 2-1; pale pollinose fascia on second tergum broadly interrupted in middle; one pair of median marginals and one or more pairs of lateral and ventral marginals on second tergum ..... *fumosa* (Townsend)
   Acrosticals 1-1; pale pollinose fascia on second tergum entire; continuous row of marginals along entire edge of second tergum ..... *aldrichi* Curran

3 (1). Without acrostical bristles 4
   At least one pair of acrostical bristles 5

4 (3). Posterior femora orange basally; median postsutural dark mesothoracic vittae separated by light vitta (seen with light striking the thorax from posterior angle) ..... *fulvibasis* Curran
   Posterior femora entirely brownish-black; median dark vittae united behind suture by dark pollen ..... *townsendi* Curran

5 (3). At least one pair of presutural acrosticals 6
   Without presutural acrosticals ..... *dives* Curran

6 (5). Three pairs of postsutural acrosticals 7
   One pair of postsutural acrosticals (occasionally a second weak pair) 11

7 (6). Acrosticals 2-3 or 3-3; median dark vittae united behind suture or dark fascia across center of entire mesoscutum except just above wings 8
   Acrosticals 1-3; median dark postsutural vittae separated for entire length by light pollen ..... *varia* Curran

8 (7). Third tergum with four discals; acrosticals 2-3, *mexicana* (Townsend)
   Third tergum with two discals; acrosticals 2-3 or 3-3 9

9 (8). Outer dark vittae fused with median dark vitta behind suture; acrosticals 3-3; body length about 8 mm. ..... *valera* Curran
   Outer dark vittae separated from median dark vitta by outer light vittae behind suture; acrosticals 2-3, rarely 3-3; body length 4 to 5.5 mm., rarely as large as 7 mm. 10

10 (9, 23). Scutellum with reddish-brown pollen confined to basal dark band; third antennal segment with basal orange color extending distally beyond insertion of arista at least as far as distance from arista to base of third segment... *panamensis* Curran

Scutellum with reddish-brown pollen over entire dorsal surface except for narrow posterior and lateral margins; third antennal segment orange from base to arista ..... *bequaerti* Curran

11 (6). Middle tibia with one or two strong ventral bristles near or beyond the middle 12

Middle tibia without ventral bristle near middle.. *fasciata* Curran

12(11). Posterior femora, when seen in ventral view, orange on at least basal fourth, abruptly becoming orange-brown to black distally and with apices usually orange; or entire femora light yellow to orange in ventral view 13

Posterior femora entirely brown to black with no abrupt change in color, the apices sometimes orange or reddish 20

13(12). Infrasquamal cilia black or absent 14

Infrasquamal cilia yellow ..... *majuscula* van der Wulp

14(13). Median pale mesonotal vitta extends to well behind suture 15

Median light mesonotal vitta absent immediately behind suture (when light strikes thorax from posterior angle) 16

15(14). Male with a row of yellow cilia on both inner and outer ventral edges of posterior femur for at least distal half; female unknown ..... *flavipes* (Shiner)

Male with a row of yellowish cilia only on inner ventral edge of posterior femur for at least distal half; both sexes with front coxae yellow-orange; sternopleural and lower mesopleural pile light yellowish to brown; female abdomen dorsally black with bluish-white pollen ..... *major* Curran

16(14). Pile of sternopleura and lower anterior mesopleura fine and white 17

Pile of sternopleura and lower anterior mesopleura rather coarse and black 18

17(16). First abdominal tergum orange with median longitudinal black stripe in female, with weak stripe or no stripe in males, *venteris* Curran

Dorsum of first tergum all black ..... *similis* (Townsend)

18(16). Outer light vittae absent behind suture or no wider than half width of outer dark vittae: fourth tergum with 2 to 4 discals 19

Outer postsutural light vittae as wide as outer dark vittae; fourth tergum with 6 to 10 discals ..... *agilis* Curran

19(18). Scutellum with three pairs of lateral marginals; fourth tergum with arched row of four discals ..... *insolita* Curran

Scutellum with two pairs of lateral marginals; fourth tergum with pair of discals (occasionally a marginal pair may look like a second pair) ..... *apicalis* Curran

20(12). Sternopleura and lower mesopleura with fine whitish hair; outer dark vittae separated from median dark vitta by light vittae behind suture 21

Sternopleura and lower mesopleura with coarser black hair; all dark vittae united behind suture or outer dark vittae separated from median dark vitta by light vittae 23

21(20). Middle femur with two anterior bristles near middle; dorsum of first tergum black, may be yellow-brown dorsolaterally in male 22

Middle femur with one anterior bristle near middle; first tergum orange with median dark stripe; female unknown, *caudata* Curran

22(21). Anterior coxae with total of about 35 (range 20 to 50) coarse black hairs and bristles and a few or no fine white hairs; third abdominal tergum of female with pale pollen extending to margin between marginal bristles .... *interrupta* Curran

Anterior coxae with total of about 12 (range 10 to 18) black hairs and bristles and numerous fine white hairs; third abdominal tergum of female with pale pollen not extending to margin between marginal bristles but small marginal spot of pale pollen may be present ..... *continua* Curran

23(20). All dark vittae united behind suture ..... *bella* Curran

Outer light vittae present behind suture (will key out above through couplet seven if all postsutural acrosticals are visible) 10

Calodexia agilis Curran

C. agilis Curran (1934a:13).

A large species (length 5.5 to 8.2 mm.) having a bluish to black abdomen without strong yellowish fascia, the mesonotum with broad postsutural outer light vittae and fused postsutural median dark vittae; the acrosticals 1-1; and the hind femora with orange bases.

Male. Unknown.

Female. Front slightly more than half as wide as eye. Ocellars usually weak, occasionally may be absent. Third antennal segment orange occasionally with browner tinge at apex. Occipital cilia extend down side of head at least two-thirds and usually three-fourths length of eye. Prementum brownish-orange to yellow-brown.

Postsutural outer dark vittae separated from median dark vitta by light vittae about equal in width to outer dark vittae; often these light vittae are narrowed to half width of outer dark vittae near

second postsutural dorsocentral. Dorsum of scutellum with basal black band and three or rarely four pairs of lateral marginals. Mesopleural hairs black, sternopleural hairs black with an occasional yellowish hair, pteropleural hairs mostly yellowish. Anterior surfaces of front coxae orange laterally, orange-brown medially; trochanters orange. Front tibiae with three to eight anterodorsal bristles; middle femur usually with two anterior bristles but sometimes one or three; posterior femora usually orange on ventral two-thirds, occasionally entirely orange ventrally.

Third tergum with light pollen extending to apex when seen in dorsal view with specimen rotated to show maximum extent of light pollen. Fourth tergum orange-brown to black in center, usually with dark vertical fascia on distal one-half to two-thirds; when dark fascia is missing entire fourth tergum is covered with white pollen; two or more bristles and numerous hairs along margin next to genital opening.

Records. Barro Colorado Island, 2 ♀ in type series (not seen). Additional records for 286 ♀ : over swarm of *Eciton vagans:* 2110 (4); over swarm raid or near *E. burchelli*: 834 (2), 991 (2), 1171 (1), 1172 (5), 1178 (2), 1411 (1), 1412 (2), 1413 (3), 1414 (11), 1415 (2), 1574 (3), 1755 (4), 1757 (5), 1778 (1), 1782 (10), 1784 (3), 1790 (2), 1849 (18), 1854 (1), 1860 (12), 2191 (6), 2230 (34), 2258-X (4), 2293 (2), 2302 (24), 2329 (18), 2341 (16); over swarm raids of *Labidus praedator*: 1277 (17), 1446 (17), 1575 (5), 1617 (2), 2068 (2), 2155 (13), 2156 (1), 2178 (5), 2179 (2), 2201 (1), 2202 (2), 2242 (14), 2257 (6); taken in laboratory: 2254-X (1).

Calodexia aldrichi Curran

C. aldrichi Curran (1934a:4).

A small species with black occipital pollen as in *C. fumosa.* Characters for separating these two species are given under *fumosa.*

Records. BRASIL: Chapada, ♀ holotype only specimen known (not seen).

Calodexia apicalis Curran

C. apicalis Curran (1934a:17).

Differs from all other *Calodexia,* when seen in dorsal view, by the broad complete black fascia behind the mesonotal suture, the bluish to black abdomen without strong yellowish fascia, the two pairs of marginal scutellars, and the single pair of discals on the fourth tergum (possibly second weaker pair close to margin).

Male. Not seen, but following changes and additions to Curran's description probably apply also to male, with possible exception of abdominal characters.

Female. Occipital pile white, black occipital cilia extend down side of head half to two-thirds length of eye. Prementum yellow-brown. Second tergum with pale pollen occupying basal three-fourths near ventral edge, narrowing to one-half laterally, narrowing to basal one-third laterodorsally, and widening to three-fourths middorsally. Third tergum with similar but slightly broader pattern of light pollen. Fourth tergum with median shining dark fascia about one-third width of tergum, as seen from below; fascia extends from base to apex and continues more narrowly along margin of tergum.

Records. Barro Colorado Island, 2 ♂, 1 ♀ in type series (not seen). Additional records for 2 ♀: over swarm raids of *praedator:* 1446 (1), 2155 (1).

Calodexia bella Curran

C. bella Curran (1934a:8).

This species is close to *fasciata* but readily distinguished by the following characters (alternatives for *fasciata* in parentheses): when seen in posterior view and posterior light, the postsutural dark fascia is narrowly continued to the wings just behind the mesonotal suture (completely interrupted above wings); there is one midventral bristle on the middle tibia (bristle lacking); there is a shining, broad, median dark fascia on the fourth tergum from base to apex (weak fascia on median posterior area of tergum and dense pale pollen basally).

C. bella was described from 13 males collected on Barro Colorado Island, and Curran (1934a: 9) suggested it might be the male of *C. fasciata,* represented in his collections by 29 females but no males. His suggestion was based largely on the dark mesonotal markings and the relative abundance of these two species. However, we found 56 females which are much closer to *C. bella* than they are to *fasciata.* Important ways in which these females differ from the male are given below. The male of *fasciata* is still unknown.

Male. Legs mostly brown with yellow to orange trochanters and orange areas on coxae. First tergum with irregular dorsolateral brownish yellow spots blending to dark brown or black in middorsum. First and second terga each with narrow yellowish band

along ventrolateral margin; second tergum (ignoring pollen) with basal one-half to two-thirds pale brownish yellow to brownish orange, brown on distal third, expanding at least to distal half middorsally where exact extent obscured by dense pollen. Third tergum similar, but brown on distal one-half to three-fourths laterally and ventrally, expanding to basal margin middorsally. Fourth tergum entirely brown; dark vitta, about one-third width of dorsum, extends to basal margin; one strong pair of discals and possibly one or two weak pairs, all in straight line or slightly arched row.

Female. Main differences from male: Head with pollen white to yellowish dorsally and in all areas whiter than in male. Front widest in center, becoming slightly narrower towards antennae and vertex.

Abdomen mostly black. First tergum black dorsally, becoming brown at ventral edge; ventrolaterally with slight trace of whitish pollen. Second tergum dark brown dorsally and lighter brown ventrolaterally; basal band of white pollen extends entire length of tergum near ventral edge, narrowing laterally to about basal half; in dorsal view white pollen narrows to about basal one-third widening medially to basal one-half to two-thirds. Third tergum similar to second but in dorsal view white pollen on basal one-third to one-half and with its posterior edge almost straight and even with discal bristles. Fourth tergum with strong median pair and usually two weaker lateral pairs of discals arranged in an arched row; discals number from three to eight and vary greatly in size and position.

Records. Barro Colorado Island, 13 ♂ in type series, 3 paratypes examined. Additional records for 1 ♂ and 55 ♀: over swarm raids or near *E. burchelli:* 827 (6), 834 (12), 944 (1), 991 (2), 1170 (1), 1172 (1), 1411 (1), 1413 (1), 1414 (2), 1574 (2), 1755 (4), 1757 (3), 1784 (1), 1790 (1), 1849 (2), 2293 (2), 2302 (7); over swarm raids of *L. praedator:* 1277 (1), 1446 (1), 1575 (1), 1617 (1), 2155 (1); sweeping on vegetation in forest: 2216 (1 ♂).

Calodexia bequaerti Curran

C. bequaerti Curran (1934a:19).

This species is extremely close to *panamensis* and distinguishing characteristics are given under that species.

Male. Unknown.

Female. Corrections and additions to Curran's descriptions follow based on examination of the holotype.

Front narrowest at bases of antennae and at that point slightly wider than width of eye. Vertex with grey-white pollen tinged with reddish brown near ocelli. Occipital pile white to yellowish. Palpus with less than ten black hairs. Third antennal segment orange from base to insertion of arista, dark brown distal to insertion of arista.

Presutural median dark vittae near mesonotal suture, about equal in width to presutural outer light vittae. Dorsum of scutellum with reddish brown or rust-colored pollen in center, or for entire dorsal surface except for margin when seen from a low anterior angle. Margin of scutellum posterior to first marginal bristles with grey-white pollen tinged with yellow. Three pairs of marginal scutellar bristles and one apical pair which is weaker than marginal scutellars but stronger than most dorsal scutellar hairs. Only one pair of postsutural acrosticals can be seen because of pin; apparently three pairs of postsutural acrosticals can been seen on one or both paratypes.

Legs brown but front trochanters and distal parts of front coxa somewhat lighter yellow-brown. Posterior lobe of squama light yellow-brown, becoming lighter toward outer edge and white at anterior base; anterior lobe white.

All terga brownish black dorsally, becoming brown ventrally. Narrow apical margins of first, second, and part of third terga yellowish ventrally. Pollen on second tergum extending in a blunt point between marginals but not reaching apex of tergum. Third segment with similar pattern. Both second and third terga may appear to have a weak median band of pale pollen extending to apex when seen at a very low posterior angle almost parallel with terga. Fourth tergum with slightly yellowish grey-white pollen on entire surface when seen in oblique dorsal view; when seen from side, tergum has two median dorso-ventral stripes of light pollen which are attenuated to fine points at apex of tergum; highly arched row of nine discals and second row of three discals near middle of tergum; about half of discals hairlike.

Records. GUATEMALA: 3 ♀ in type series, holotype examined.

Calodexia caudata Curran

C. caudata Curran (1934a:16).

Although this species resembles *similis*, the first and second terga are orange (compared to brown or black in *similis*). *C. caudata* is also similar to *venteris*, but has brownish hind femora, and the head has dense white pollen (compared with yellow to light orange

hind femora and gold pollen on dorsal areas of the head in *venteris*).

Records. PANAMA: Cabima, 1 ♂ holotype (not seen).

Calodexia continua Curran

C. continua Curran (1934a:10).

C. continua can be distinguished from *interrupta*, the most similar species, by the numerous white hairs and the 10 to 18 black hairs and bristles on the anterior surface of the front coxa; the third tergum which has a pale band of pollen not extending to the apex between the median marginal bristles; and the middle tibia which usually has two ventral bristles near the middle.

Female. Front more than half as wide as eye. Black occipital cilia extend down side of head at least one-half and usually two-thirds length of eye. Prementum orange to brown. Palpus orange to yellow-brown. Third antennal segment orange at base, becoming orange-brown at apex.

Outer dark vittae continued to anterior face of thorax but usually narrowed beyond median sublaterals. Median dark vittae fused behind suture. Postsutural outer dark vittae separated from median dark vitta by narrow pale vittae about one-fourth as wide as outer dark vittae. Postsutural outer light vittae often reduced or incomplete near middle postsutural dorsocentrals. Anterior surface of front coxa orange to brown, with numerous long, fine, white hairs and total of 10 to 18 black hairs and bristles. Middle tibia with one long ventral bristle shortly beyond middle and usually one shorter bristle closer to middle.

First tergum with ventrolateral white pollen about as dense as ventrolateral pollen on second tergum. Third tergum with pale pollen extending at most about half way from discals to apex, small marginal spot of pale pollen may be present but not continuous with basal light pollen. Fourth tergum with eight to ten discals in highly arched row and occasionally additional weak discals. Fourth tergum has vertical fascia without pale pollen; color of tergum usually orange, occasionally all brown.

Records. Type series of 16 ♀ : Barro Colorado Island, 14 ♀ ; CANAL ZONE: Cano Saddle, 1 ♀ ; and GUATEMALA, 1 ♀ . Three paratypes from Barro Colorado Island examined (1 ♀ paratype, 5812, in Snow Entomological Museum, University of Kansas). Additional records for 119 ♀ : over swarm raids or near *E. burchelli*: 834 (3), 991 (1), 1171 (1), 1172 (1), 1178 (2), 1411 (1), 1412

(2), 1413 (2), 1414 (3), 1415 (1), 1574 (6), 1755 (5), 1757 (11), 1782 (4), 1784 (2), 1790 (5), 1849 (13), 1860 (2), 2191 (3), 2230 (7), 2258-X (1), 2293 (2), 2302 (4), 2341 (3); over swarm raids of *praedator*: 1277 (18), 1446 (10), 1617 (4), 2242 (2).

Calodexia dives Curran

C. dives Curran (1934a:6).

The large size (6.0 to 9.0 mm.), bluish black abdomen, median dark vittae fused behind the suture, completely dark femora, white hairs on front coxae and most of pleura, and lack of presutural acrosticals separate this species from all other *Calodexia*.

Male. Unknown.

Female. Front more than one-half as wide and usually about three-fourths as wide as eye. Black occipital bristles extend down side of head about two-thirds length of eye. Third antennal segment orange, becoming orange-brown or brown at apex.

Median dark vittae united into single vitta behind suture, but few spots of light pollen occasionally present in center of this vitta. Behind suture outer light vittae about one-half as wide as outer dark vittae. Outer dark vittae continued to anterior surface of thorax but usually narrowed in front of median sublaterals. Scutellum with three, or occasionally four, pairs of lateral marginals; apical marginals absent, hair-like, or strong (but never as strong as posterior laterals). Front coxa orange to orange-brown, with fine white to yellowish hairs and 10 to 18 black hairs and bristles.

Third tergum with pale pollen extending to apex between median marginal bristles, except in a few specimens. Fourth tergum with arched row of 6 to 12 discals; entire surface covered with whitish pollen when seen from posterior dorsal view; when observed perpendicularly to surface of tergum only lateral basal areas show dense whitish pollen.

Records. Barro Colorado Island, 20 ♀ in type series (none seen). Additional records for 198 ♀: near *E. burchelli* or over its swarm raids: 834 (3), 1171 (1), 1172 (1), 1411 (3), 1412 (3), 1413 (9), 1414 (14), 1415 (5), 1755 (7), 1756 (1), 1757 (2), 1782 (2), 1790 (2), 1849 (4), 2230 (2), 2341 (1); over swarm raids of *L. praedator:* 1277 (28), 1446 (68), 1575 (18), 1671 (6), 2068 (3), 2155 (7), 2178 (1), 2201 (1), 2242 (4), 2257 (2).

Calodexia fasciata Curran

C. fasciata Curran (1934a:5).

This species can be distinguished from all other *Calodexia* by the white occipital pollen, the lack of ventral bristles near the middle of the middle tibia, and the postsutural dark fascia which is completely interrupted above the wings when seen in posterior view with posterior light. (In the most similar species, *bella*, this fascia is narrowly continued to the wings just behind the mesonotal suture.) The fourth tergum, from the margin at the posterior end of the opening for the larvipositor to the median basal margin, is about twice as long as broad and has dense yellowish pollen between the discals and the basal margin. (In *bella*, this same area of the fourth tergum is slightly broader than long, and the shining, dark fascia extends to the median basal margin.)

Male. Unknown.

Female. Front slightly more than one-half as wide as width of eye. Black occipital cilia extending down side of head one-half to three-fourths length of eye.

Weak outer light vittae sometimes partially separate postsutural median dark vitta from outer dark vittae. Dorsocentrals 2-3, occasionally 3-3. Acrosticals 1-1, in addition occasionally one or two weaker presutural pairs and one weaker postsutural pair. Front coxae orange to dark brown. Hind femur, seen ventrally, with basal one-fourth to one-third orange, occasionally entire femur orange to orange-brown.

First tergum orange-brown to black; first and second terga each with one strong pair and usually one or more weaker lateral pairs of marginals. Dorsum of third tergum with posterior edge of pale pollen approximately straight. Fourth tergum about twice as long as broad, with high narrow arch of 7 to 14 discals, some frequently scattered outside row or in second row; color of tergum from orange to yellow-brown to black; dense pale pollen along basal margin but less dense within row of discals.

Records. Barro Colorado Island, 29 ♀ in type series (none seen). Additional records for 244 ♀ : over swarm of *E. vagans:* 2110 (1); over swarm raids of *E. burchelli*: 367 (2), 827 (3), 834 (28), 944 (2), 1170 (1), 1171 (4), 1172 (3), 1178 (19), 1411 (4), 1412 (3), 1413 (4), 1414 (6), 1415 (1), 1570 (1), 1574 (3), 1755 (21), 1757 (6), 1782 (9), 1784 (7), 1790 (7), 1849 (20), 1860 (1), 2191 (1), 2230 (14), 2293 (1), 2302 (11), 2329 (1), 2341 (7); over

swarm raids of *L. praedator*: 1277 (9), 1446 (12), 1575 (5), 1617 (10), 2068 (1), 2155 (3), 2178 (2), 2242 (3), 2257 (8).

Calodexia flavipes (Schiner)

Meigenia flavipes Schiner (1868:326) ♂.
Calodexia flavipes, Brauer and Bergenstamm (1891:376). Aldrich (1929:22-23) redescription of ♂; ♀ = *Calodexia varia.*

This species is similar to *major* which may be synonym of *flavipes* as explained under *major.*

Records. BRASIL, Novara Expedition, exact locality unknown, 1 ♀.

Calodexia fulvibasis Curran

C. fulvibasis Curran (1934a:7) ♀.

Calodexia townsendi and *C. fulvibasis* are the only two species in the genus lacking all acrosticals. The latter species can be distinguished from *townsendi* by the median dark vittae which are separated for their entire length; the orange bases of the posterior femora; and the four discals on the fourth tergum.

Records. PERU: Jaen Province: Huascaray Ridge: 7000 feet, 1 ♀ (not seen).

Calodexia fumosa (Townsend)

Oestrogaster fumosus Townsend (1912:310). Townsend (1914:28), correction of description.
Calodexia fumosa, Aldrich (1929:21). Curran (1934a:5).

Both *C. aldrichi* and *fumosa* have black occipital pollen and a large dark fascia across the entire thorax behind the suture. These two species can be separated by the following characters (the alternatives for *aldrichi* in parentheses): The band of pale pollen on the second tergum is broadly interrupted in the middle (not interrupted); the second tergum has a pair of median marginals (row of marginals); and the acrosticals are arranged 3-1 or 2-1 (1-1).

The specimens from Barro Colorado Island reported by Curran and my specimens from the same locality, which have been partially determined by him, apparently belong to the same species. However, slight differences in size, color, and morphology may indicate that the Panamanian specimens are not *fumosa*, but a new species.

Male. Unknown.

Female. Not redescribed by Curran. Specimens examined differ from original description in following manner: Seven to nine pairs of frontal bristles including two proclinate and two reclinate fronto-

orbital pairs in line with frontals; ocellar bristles fine and hair-like; palpi yellow with few short black hairs; antennae yellow to brown. Scutellum with two or usually three marginals. Second abdominal segment with one pair of discals.

Records. PERU: Jaen Province: 5000 feet; on foliage, holotype ♀ (not seen). Barro Colorado Island, 21 ♀ reported by Curran (1934a:5); additional records for 85 ♀ : over swarm raids of *E. burchelli*: 827 (2), 834 (3), 1172 (2), 1178 (4), 1411 (1), 1412 (2), 1574 (3), 1755 (1), 1782 (1), 1790 (1), 1849 (1), 2230 (3); over swarm raids of *L. praedator:* 1277 (29), 1446 (10), 1575 (6), 1617 (4), 2155 (1), 2178 (3), 2201 (1), 2202 (1), 2242 (2), 2257 (4).

Calodexia insolita Curran

C. insolita Curran (1934a:4, 15), key. Curran (in Curran, et al. [1934:506]).

Although close to *apicalis,* this species can be separated by the scutellum which has three pairs of lateral marginals, and the fourth tergum which has an arched row of four discal bristles. (The latter is not a generic character as stated in Curran, et al. [1934:506]).

Records. BRITISH GUIANA: Kartabo, holotype ♀ (not seen).

Calodexia interrupta Curran

C. interrupta Curran (1934a:9).

This species is similar to *continua* but easily distinguished from it by the pale pollen extending to the apex of the third tergum between the median marginals. (In *continua* the pale pollen does not extend medially to the apex, but a small marginal spot of light pollen is sometimes present and not connected with the basal band.) The pleural pile is white, and the anterior surface of each front coxa has a few white hairs and 25 to 35 black hairs and bristles.

Male. Front, at narrowest point near its center, slightly less than half as wide as eye and widening at bases of antennae to more than two-thirds as wide as eye. No proclinate orbitals; ten pairs of frontals including two upper reclinate fronto-orbital pairs. Black occipital cilia extending down side of head two-thirds length of eye.

Outer and inner dark vittae usually at least partially interrupted at suture. Front coxae brown with some brownish orange laterally; hind femora entirely brown to black except for tips, which are somewhat orange. Middle and hind femora each with row of long golden-brown hairs along outer two-thirds of posterior ventral margins; similar shorter row along anterior ventral margin of hind

femur. Third tergum with pale pollen usually extending as a narrow band between median marginals to apex. Fourth tergum with curved row of seven to eight discals approximately parallel with posterior edge of second tergum.

Female. Lower two-thirds of front with parallel sides and about two-thirds as wide as eye; front narrowed toward vertex but remaining more than one-half as wide as eye. Two pairs of proclinate orbitals; six to eight pairs of frontals. Apical scutellar bristles hairlike or absent. Middle femur with usually two (occasionally one or three) anterior bristles near middle. Middle tibia with one, very rarely two, ventral bristles near middle. Third tergum with basal band of light pollen expanded medially to apex; between median marginals pale pollen at least half as wide as distance between marginals. Fourth tergum with dense whitish pollen along basal margin; dark fascia extending from distal margin of tergum one-half to three-fourths distance to base; discals scattered or arranged in one very irregular row of 8 to 12 bristles.

Records. Barro Colorado Island, 2 ♂ and 15 ♀ in type series; 1 ♂, 3 ♀ paratypes examined (1 ♀ paratype, 5813, in Snow Entomological Museum, University of Kansas). Additional records for 6 ♂ and 170 ♀: over swarm of *E. vagans:* 2110 (5 ♀, 1 ♂); near *E. burchelli* or its swarm raids: 834 (4), 991 (1), 1178 (2), 1413 (1), 1414 (1), 1574 (1), 1755 (3), 1757 (2), 1782 (7), 1790 (3), 1849 (6), 1860 (15), 2191 (8), 2230 (17), 2258-X (2), 2302 (6), 2329 (11), 2331 (1), 2341 (14); over swarm raids of *L. praedator:* 1277 (5), 1446 (4), 1575 (1), 1617 (12), 2068 (1), 2155 (1), 2178 (9), 2179 (4), 2201 (10), 2202 (2), 2206 (1), 2242 (4), 2257 (1); reared from cricket escaping from swarm raid of *E. burchelli:* 2260-X (4 ♂, 4 ♀); taken in laboratory: 1552 (1), 2346 (1 ♂).

Calodexia major Curran

C. major Curran (1934a:12).

This is one of the larger species (6.8 to 8.9 mm.). The hind femur has at least the basal half orange, and the postsutural median dark vittae are separated by light pollen. The female has a bluish black abdomen and the third tergum has pale pollen extending from the median marginals to the apex. The males have reddish first and second terga.

The males according to Curran (1934a: 3, 11-12) also have a single row of long yellow cilia along almost entire length of the *posterior* ventral margin of each hind femur. The two male specimens ex-

amined have a weaker row of the same type hairs along the distal one-fourth to one-third of the *anterior* ventral margin of the hind femur. The presence of a single row of ventral cilia on the hind femur of the male is the only character used by Curran to separate *C. flavipes* (Schiner) from *major*. Curran did not see the type of *flavipes* but examined one specimen from the U. S. National Museum which had been compared with the type and was considered to be identical by Aldrich. However, Curran found that that specimen did not agree with the original description of *flavipes*, and he decided that *major* was a distinct species. No sound conclusion can be reached on this problem without re-examination of the type of *flavipes*.

Male. Front narrowest at level of ocelli where 2/7 to 2/9 as wide as eye; width of front doubled at level of antennae. No proclinate fronto-orbitals. Black occipital cilia extending downward two-thirds length of eye.

All mesonotal vittae may be partially interrupted at suture. Apical scutellars hair-like or absent. Sternopleura with yellowish white hairs; mesopleura with yellowish white hairs on central and antero-ventral areas, and dark brown to black hairs along antero-dorsal, dorsal, and posterior margins. Notopleura with dark hairs. Coxae mostly orange with small areas of orange-brown, and with yellowish white and brown or black hairs. Hind femur with one row of long yellow hairs along almost entire length of posterior ventral margin and second weaker row along distal one-fourth to one-third of anterior ventral margin.

First tergum with ventral and lateral areas pale brownish yellow to pale brownish orange; darker brown median stripe continued along apical margin laterally to lateral marginals.

Female. Two proclinate fronto-orbitals and seven to eight pairs of frontals (including two pairs of reclinate fronto-orbitals). Front coxae as given above for male. Middle femur with two or occasionally one anterior bristle near middle. Posterior femur with approximately basal half orange and distal half orange-brown or occasionally with entire femur orange-brown. Hind femora without long yellow ventral cilia.

Fourth tergum with one highly arched row of discals and occasionally second partial row or some scattered bristles outside of main row.

Records. Type series of 3 ♂, 15 ♀: Barro Colorado Island, 2 ♂, 14 ♀; PANAMA: Gatun Lake: Cano Saddle, 1 ♀; COSTA

RICA: La Suiza, 1 ♂ (none seen). Additional records for 2 ♂, 43 ♀: over swarm raids of *E. burchelli:* 834 (8), 1411 (1), 1414 (1), 1419 (1), 1574 (1), 1782 (1), 1784 (1), 2191 (1), 2230 (2), 2258-X (2), 2302 (4), 2329 (3), 2341 (3); over swarm raids of *L. praedator:* 1277 (2 ♀, 1 ♂), 1446 (5), 1617 (2), 2155 (1 ♀, 1 ♂), 2178 (1), 2179 (1), 2201 (1), 2242 (1).

Calodexia majuscula van der Wulp

C. majuscula van der Wulp (1891:257-258, pl. 6, figs. 12, 12a) ♂; figs. of side of head, dorsal view including wings. Coquillett (1910:517) designated type species (first of three species described by van der Wulp [1891]). Aldrich (1929:21-22) redescription based on ♂ which had been compared with type. Curran (1934a:13).

This species is distinct from all other *Calodexia* since it has pale infrasquamal cilia, and the abdomen is mainly yellow to orange with a strong dark median stripe on both the first and second terga.

The diagnostic character, presence of pale infrasquamal cilia, used to separate this species, is taken from the redescription by Aldrich (1929) based on a specimen which had been compared with the type by Major Austen. The figure of the dorsal view (van der Wulp, 1891: pl. 6, fig. 12) shows a broad pale median vitta behind the mesonotal suture. This may not be present when seen from posterior view with posterior light.

Records. MEXICO: Tabasco: Teapa; ♂ holotype; Morelos: Cuernavaca, 1 ♂ (Aldrich, 1929) (not seen).

Calodexia mexicana (Townsend)

Oestrogastropsis mexicana Townsend (1915:424-425) ♀.
Calodexia mexicana, Aldrich (1929:21). Curran (1934a:21).

This is a medium to large species with three postsutural acrosticals as in *varia* and *valera.* It differs from these two species by having two presutural acrosticals and four discals on third tergum.

There can be little doubt that this is a distinct species. Curran examined the type and separated *mexicana* in his key by the presence of acrosticals 2-3 (not mentioned by Townsend). The original description will fit almost all species in *Calodexia* except for the unusual number of four discals on the third tergum.

Records. MEXICO: Veracruz, ♀ holotype (not seen).

Calodexia panamensis Curran

C. panamensis Curran (1934a:18).

A small species close to *bequaerti* from which it can be distinguished by the following characters (alternatives for *bequaerti* in parentheses): The third antennal segment is brown except for

some orange near the base. The orange color is continued, on at least the medial side of the segment, to a point at least as far beyond the insertion of the arista as the latter is beyond the base of the segment (the orange color extends only from the base of the third segment to the insertion of the arista). In addition, the vertex has shining yellowish white pollen (duller yellowish grey-white pollen on the vertex with a red-brown tinge near ocelli); the scutellum, when seen in oblique anterior view, has reddish brown or rust-colored pollen confined to a basal dark band (reddish brown pollen over the entire dorsal surface except for the posterior and lateral margins); in perpendicular dorsal view the anterior border of light pollen on the scutellum appears to be straight (anterior border of light pollen concave, parallel to the apical scutellar margin).

In comparing the holotype of *bequaerti* with my series of *panamensis* the following characters used by Curran (1934a: 18-19) were found to show no reliable interspecific differences: total length; relative length of outer verticals; color of frontal vittae, squamae, abdomen, and legs; number of marginal scutellar bristles; and patterns of pale pollen on the abdominal terga.

Male. No specimens examined.

Female. Front as wide or slightly wider than either parafrontal; six to nine pairs of frontals; outer verticals more than half as long as verticals.

Apices of first, second, and part of third terga yellowish on ventral surface. Light pollen on second tergum extends in middle from base to median marginal bristles or to apex; pale pollen occupies basal one-half to two-thirds of tergum dorsolaterally, and widens to at least three-fourths at ventral margin. Third tergum with pattern of pollen as in second or with slightly broader band of pale pollen with straighter posterior edge. Fourth tergum with slightly yellowish gray-white pollen on entire surface when seen in oblique dorsal view; when seen from side, tergum has two median dorsoventral stripes of light pollen which are attenuated to fine points at apex of tergum; about ten discals arranged in highly arched row, and about three additional discals in second row near middle of tergum, occasionally discals in three indistinct rows; about half of discals are hair-like.

Records. Type series of 3 ♂ and 4 ♀: Barro Colorado Island, 2 ♂, 2 ♀; CANAL ZONE: Cano Saddle, 2 ♀, Tabernilla, 1 ♂ (none seen). Additional records for 29 ♀: over swarm raid of *E. bur-*

chelli: 1782 (2); over swarm raids of *L. praedator:* 1277 (3), 1446 (9), 1575 (6), 1617 (2), 2155 (2), 2179 (3), 2242 (1), 2257 (1).

Calodexia similis (Townsend)

Oestrogastrodes similis Townsend (1915:425) ♀.
Calodexia similis, Aldrich (1929:21). Curran (1934a:14).

Although close to *agilis, continua,* and *interrupta,* this species can be separated by the white hairs on the pleura together with the bases of the posterior femora appearing orange when seen in ventral view.

These structures, used by Curran (1934a: 14) were separating *similis* from *agilis,* are found in both species or are too variable to be of value: ocellar bristles, anterior dorsal bristles on the front tibiae, and marginal bristles on the fourth tergum.

The male of *similis* is described here for the first time. Because Curran did not redescribe *similis* and Townsend's description is very incomplete, a more complete description of the female is also included.

Male. Head with dense white pollen becoming gold on parafrontals and upper posterior orbits. Background color of cheek (ignoring pollen) orange-brown; parafacials orange becoming brown on front. Sides of front straight and diverging; front narrowest at vertex where slightly wider than half width of eye; at dorsal edges of antennal bases front almost as wide as eye. Frontal vitta dark reddish brown to black and about as wide as parafrontals. Nine pairs of frontals, including two pairs of reclinate fronto-orbitals and two pairs of proclinate fronto-orbitals. Ocellars strong (for *Calodexia*), as long or longer than width of frontal vitta at widest point. Occipital pollen and pile white or slightly yellowish; median and dorsal dark areas in pollen. Black occipital cilia extend downward three-fourths length of eye. Prementum light yellowish brown. Palpus swollen club-like, distal half more than twice diameter of basal half; with more than 25 short black hairs, fewer scattered long yellow hairs, and dense covering of short pale pile merging into pollen basally. Entire antenna dark brown except for lighter brown arista and lighter more orange areas on second segment and base of third segment below arista. Arista with longest dorsal hairs about twice as wide as arista at widest point, ventral hairs shorter than width of arista.

Thorax with white pollen becoming pale yellowish on dorsum. Presutural median dark vittae about three-fourths as wide as pre-

sutural outer light vittae. Presutural outer dark vittae more than twice as wide as outer light vittae and extended broadly to anterior surface of thorax. Median dark vittae not interrupted at suture; outer dark vittae interrupted laterally by an indentation of light pollen. Median dark vittae united behind suture into a broad median vitta which narrows in middle of scutum and extends posteriorly as more gray and indistinct narrow median stripe to scutellum. Postsutural outer light vittae about half as wide as outer dark vittae. Scutellum with basal dark band, three pairs of marginal scutellars, and one weak hair-like apical pair. Pile on pleura white except for anterodorsal, dorsal, and posterior margins of mesopleura which have some dark hairs. Notopleuron with about six black hairs. Subsquamal cilia black. Acrosticals 1-1; anterior intra-alar strong.

Anterior surface of front coxa with outer orange band, inner brown band, about 30 to 40 black hairs and bristles, and many thin yellowish hairs. Basal one-half to three-fourths of each middle and hind femur orange in ventral view. Middle femur with two anterior bristles near middle; middle tibia with single ventral bristle somewhat beyond middle. Posterior femur with row of brown hairs along only about distal third of inner posterior margin; at apex of femur these hairs about as long as width of hind tibia, becoming shorter toward base of femur. No yellow cilia on hind femur.

Abdomen black with grey-white ventrolateral pollen becoming tinged with yellow dorsally. First tergum black and with no pale pollen in dorsal view; ventrolaterally with white pollen present but less dense than on same area of second tergum. Second tergum with narrow median dark stripe and dark patches around discals; white pollen bordering stripe for basal two-thirds of tergum, pollinose area narrowing abruptly to less than basal one-fourth on more lateral areas of dorsum, widening to about basal two-thirds at level of lateral bristles, and widening to at least three-fourths ventrally. Third tergum with triangle of whitish pollen extending to apex medially but weak between marginals; when viewed at a low posterior angle, almost parallel to the tergum, a median dark stripe can be seen; laterally pattern of pollen is like that of second tergum. Fourth tergum reddish brown but completely covered with light pollen in most views; slight trace of narrow median dark vitta; one row of four to six discals; second and third terga each with one pair of discals. First and second terga each with one pair of median and one pair of lateral marginals; third and fourth each with a

row of marginals. Hairs black, except white on first abdominal sternum (first morphological segment) and ventrolateral areas of first tergum.

Female. Differs from male as follows: Pollen on upper parts of head less golden, but more yellowish gray-white. Front narrowest at vertex where almost two-thirds as wide as eye. Front widening in middle, becoming slightly narrower below, and then widening again at bases of antennae; at widest points in middle and at bases of antennae about three-fourths as wide as eye. Frontal vitta one-half as wide as to slightly wider than parafrontals. Nine to 11 pairs of frontals including fronto-orbitals. Black occipital cilia extend downward at least one-half and usually two-thirds length of eye. Prementum orange-brown. Palpus of about equal diameter for entire length. Antenna with basal segments orange to brown; third segment orange for at least basal one-third and brown distally. Longest hairs on arista two to three times width of arista at widest point.

Thorax with presutural median dark vittae equal in width or slightly narrower than presutural outer light vittae. All dark vittae narrowly interrupted at suture. Postsutural median dark vitta not continued to scutellum. Apical scutellars may be absent.

Anterior surface of front coxa with seven to ten black hairs and bristles and many thin white or yellowish hairs. Row of brown hairs on inner posterior margin of hind femur present but sometimes less distinct than in male.

First tergum with traces of light pollen visible in dorsal view; ventrally with white pollen almost equal in density to that on second tergum. Second and third terga without median dark stripes. Light pollen on basal two-thirds of second tergum medially, pollinose area narrowing only slightly to dorso-lateral angle of tergum; ventrally light pollen may occupy basal three-fourths of tergum. Third tergum similar to second of female but with pale pollinose area extending to apex between median marginals. Fourth tergum black, completely pale pollinose, or median dark fascia may occupy distal one-half to two-thirds of tergum; one highly arched row of 9 to 14 discals and sometimes second row of two to three discals. Ventral white hair more numerous than in male and also found on second abdominal tergum.

Records. Type series of 2 ♀ : PANAMA: Arajan [= Prov. Panamá: Arraiján ?] 1 ♀ ; MEXICO: Veracruz: San Rafael: near Jicaltepec, 1 ♀ . PANAMA: Canal Zone: Barro Colorado Island,

2 ♀, (Curran, 1934a: 14); additional records for 2 ♂, 107 ♀: over swarm of *E. vagans:* 2110 (1); near *E. burchelli* or its swarm raids: 834 (4), 944 (1), 991 (1), 1170 (1), 1171 (2), 1172 (9), 1178 (1), 1394 (1), 1412 (1), 1413 (8), 1414 (5), 1415 (4), 1574 (4), 1755 (5), 1757 (5), 1782 (4), 1784 (1), 1849 (3), 1860 (2), 2191 (2), 2230 (4), 2302 (4), 2329 (3), 2341 (2); over swarm raids of *L. praedator*: 1277 (5), 1446 (8), 1575 (3), 1576 (2 ♂), 1617 (2), 2155 (2), 2178 (1), 2242 (3), 2257 (2); taken in laboratory: 1940 (1).

Calodexia townsendi Curran

C. townsendi Curran (1934a:7) ♀.

This species lacks all acrosticals like *fulvibasis* but differs from the latter by having the median dark vittae united behind the mesonotal suture, blackish hind femora, and six discals on the fourth tergum.

Records. PERU: Jaen Province: Huascaray Ridge: 7000 feet, ♀ holotype (not seen).

Calodexia valera Curran

C. valera Curran (1934a:19) ♂.

Although close to *panamensis* and *varia, Calodexia valera* can be easily identified by its having acrosticals 3-3, and by the black mesonotal vittae which are all united behind the suture.

Records. VENEZUELA: Valera, 1 ♂ (not seen).

Calodexia varia Curran

C. flavipes, Aldrich (1929:23-24) ♀ description, misidentification.
C. varia Curran (1934a:20).

C. varia is another large species (6.3 to 7.8 mm.) with a bluish abdomen similar to that of *agilis, apicalis, dives, major,* and *similis.* However, it differs from these species by the presence of a median light vitta extending the entire length of the mesonotum; the scutellum lacks a basal dark band, is entirely covered with whitish pollen, and has three pairs of marginal scutellars.

Male. Unknown.

Female. Front narrowest at vertex and almost three-fourths as wide as eye; front only slightly wider in middle; frontal vitta reddish brown to black, slightly narrower to wider than either parafrontal. Third segment of antenna orange at least from base to insertion of arista and sometimes for about basal third, distally orange-brown to dark brown.

Third tergum with at least one pair of median discals, sometimes up to nine discals in transverse row. When four or more discals are present usually a lateral discal pair is present in addition to median discal pair. ("Median discals" are in usual dorsal position and "lateral discals" are same distance from basal margin but on lateral part of tergum directly anterior to lateral marginals.) Fourth tergum has strong row of 6 to 12 discals and may have second discal row of about two bristles.

Records. Barro Colorado Island, 1 ♀ holotype. COSTA RICA: Higuito, 1 ♀ described by Aldrich (1929: 23-24) as the female of *C. fasciata* (neither seen). Additional records for 10 ♀: over swarm raids of *E. burchelli:* 1172 (1), 1418 (1), 1755 (1), 2302 (1); over swarm raids of *L. praedator:* 1277 (1), 1446 (2), 2179 (1), 2201 (1); sweeping on vegetation in forest: 1723 (1).

Calodexia venteris Curran

C. venteris Curran (1934a:15) ♀.

Only *C. majuscula* and *venteris* have a yellow to orange abdomen with a median dark stripe. *C. venteris* differs from *majuscula* by having black infrasquamal cilia. In the male all four abdominal terga are orange, the third with a brown marginal stripe composed mainly of dark brown spots at the bases of the marginals. The first tergum of the female is orange with a strong median brown stripe; the second tergum is orange with a wider median brown stripe continued as an apical brown stripe; the third and fourth terga are brown dorsally.

Two males and one female were reared from larvae removed from a *Calodexia venteris* female and introduced into a puncture made in the abdomen of a cockroach. The male description given below is based on these reared specimens which must belong to *venteris* unless this species is a complex of several similar species.

Male. Agrees with description of female (Curran, 1934a: 15-16) except as follows: Head with white pollen becoming gold above antennae and on upper occiput; background colors (ignoring pollen): orange on cheek; darker reddish orange and brown on front; and orange-brown, red-brown, or brown on occiput. Front narrowest in middle where about one-fourth as wide as eye; at vertex and bases of antennae one-third to one-half as wide as eye; 10 to 11 pairs of frontals, lower six to nine pairs decussate, remaining upper pairs reclinate. Black occipital cilia extend downward one-half to two-

thirds length of eye. Outer verticals less than half as long as verticals and far back on head in line with occipital cilia. Inner verticals decussate or sloping together at tips. Palpus with scattered long fine yellowish hairs, 10 to 30 coarser black hairs, and dense covering of short closely appressed fine yellow hairs. Antenna entirely yellow except for arista which is orange at base and brown to black distally.

Humeri with gold pollen; pollen on upper mesopleura yellowish. Middle marginal scutellar weak or absent. Coxae and femora light yellow to orange and lighter than in female. Coxae with fine white to yellow hair. Middle femur with one anterior bristle near middle; hind femur with row of long yellow cilia on inner ventral margin.

All terga entirely orange except: first may have faint median brown stripe, third has brown spots at bases of marginals which tend to fuse into brown apical stripe. First tergum without pollen; other terga with inconspicuous white pollen ventrally, becoming yellow to gold dorsally. Second tergum with white pollen usually visible only laterally and on less than basal fourth; indistinct wider band of yellow pollen dorsally. Similar band along basal one-half to two-thirds of third tergum, becoming somewhat wider medially. Fourth tergum dorsally with yellow pollen on basal one-half to two-thirds, pollinose area increasing ventrally to apical margin. First and second terga each with pair of median and pair of lateral marginals; third with row of 11 to 12 marginals; fourth tergum with row of 12 marginals; marginals on all four terga of about equal size. Fourth tergum with row of six discals in center of tergum. Genitalia yellow to orange.

Female. Specimens agree with description by Curran except: Front about two-thirds as wide as eye. Black occipital cilia extend downward one-half to two-thirds length of eye. Palpus as described above for male. Third segment of antenna yellow to orange with brown color varying from faint apical tinge to brown on distal two-thirds.

Middle femur with two anterior bristles near middle (about two percent of females have one bristle on one or both middle femora).

Pollen on all terga white ventrally, becoming yellow to gold dorsally. In ventral view abdomen appears yellow to reddish orange; apical brown band on second tergum usually does not extend for more than lateral half of ventral surface; apical brown band on third terga wider and usually extends almost to ventral edge. First and second terga each with pair of median and pair of lateral marginals.

Records. Type series of 29 ♀: Barro Colorado Island, 28 ♀: COSTA RICA: Higuito, San Mateo, 1 ♀; (none seen). Additional records for 2 ♂, 441 ♀: over swarm of *E. vagans:* 2110 (6); near *E. burchelli* or over its swarm raids: 367 (2), 827 (6), 834 (21), 944 (2), 991 (1), 1170 (16), 1171 (11), 1172 (12), 1178 (15), 1411 (4), 1412 (2), 1413 (3), 1414 (6), 1569-A (1), 1574 (2), 1750 (2), 1755 (14), 1757 (6), 1782 (18), 1784 (4), 1790 (6), 1849 (12), 1854 (4), 1860 (6), 2191 (12), 2230 (54), 2258-X (9), 2302 (40), 2329 (20), 2331 (4), 2341 (30); over swarm raids of *L. praedator:* 1277 (11), 1446 (10), 1575 (5), 1617 (8), 2068 (2), 2155 (10), 2178 (6), 2179 (2), 2201 (7), 2202 (4), 2242 (8), 2257 (16); reared from larvae artifically introduced into cockroach: 2236 (2 ♂, 1 ♀).

LIST OF FIELD NUMBERS WITH COLLECTING DATA FOR FLIES

The date, time and other important data are given below for all the flies collected in order to save space in preceding pages. The lists are arranged in order of field number under three main headings for flies associated with (1) *Labidus praedator,* (2) *Eciton burchelli,* (3) other ants or those flies taken which were not associated with any ants. All specimens were collected on Barro Colorado Island, Canal Zone, Panama, by the author and his wife, Marian E. Rettenmeyer, except for specimens with 1952 and 1955 dates which were taken by the author alone. The total number of specimens is given for the three genera discussed in this paper: *Stylogaster* (*S.*), *Calodexia* (*C.*), and *Androeuryops* (*A.*). All field numbers with letters after them (*e. g.,* 2341-A) have the same data in this list as the same numbers without the letter, except for those followed by the letter X which have different data.

Associated with *Labidus praedator*

All specimens were taken over swarm fronts or up to two meters in advance of the ants except where other data are given.

465—25 April, 1952, 1:00 p. m., 1 *S.*

1277—27 February, 1956, 1:00 to 2:00 p. m., raid swarm stopped about 1:45 p. m., 5 *S.*, 130 *C.*, 11 *A.*

1446—15 March, 1956, 1:00 to 1:15 p. m., raid swarm unusually large, more than five meters wide at front, 7 *S.*, 157 *C.*, 6 *A.*

1575—27 March, 1956, 10:55 to 11:00 a. m., 1 *S.*, 50 *C.*, 8 *A.*

1576—27 March, 1956, 11:10 to 11:15 a. m., same raid as 1575, but flies seen flying repeatedly over a cockroach; whether larvae were deposited could not be determined; 2 *C.*

1617—6 April, 1956, 10:55 to 11:05 a. m., 7 *S.*, 53 *C.*, 9 *A.*

2068—5 July, 1956, 10:30 to 11:00 a. m., 9 *C.*

2155—21 July, 1956, 12:15 to 1:00 p. m., taken one to two meters in advance of swarm front, 43 *C.*, 7 *A.*

2156—21 July, 1956, about 12:15 p. m., same raid as 2155, 1 *C.*
2178—25 July, 1956, 10:00 to 10:15 a. m., 28 *C.*, 1 *A.*
2179—25 July, 1956, 11:00 to 11:15 a. m., same raid as 2178, 1 *S.*, 13 *C.*
2201—27 July, 1956, 9:55 to 10:05 a. m., small swarm front only one to two meters wide, field numbers 2202, 2206, 2207 from same raid, 1 *S.*, 22 *C.*, 1 *A.*
2202—27 July, 1956, 9:55 to 10:05 a. m., 9 *C.*
2206—27 July, 1956, 11:15 to 11:20 a. m., taken by sweeping over entire area of raid seen from 9:55 to 10:20. Raid swarm stopped at 10:20, but workers continued to tear apart booty and were seen running along raid columns to several holes in the ground up until 11:10. 1 *C.*
2207—27 July, 1956, 10:10 a. m., taken *in copulo* on leaf 15 cm. above ground, 2 *A.*
2242—31 July, 1956, 10:00 to 11:00 a. m., sweeping quite intermittently over swarm, 6 *S.*, 42 *C.*
2257—1 August, 1956, 1:00 to 1:15 p. m., 40 *C.*, 1 *A.*
2258—1 August, 1956, same raid as 2257, may have been *in copulo*, 2 *S.*

Associated with *Eciton burchelli*

All specimens were taken over swarm fronts or up to two meters in advance of the ants except where other data are given.

367—1 April, 1952, 12:30 p. m., 4 *C.*
827—10 February, 1955, 10:30 to 10:40 a. m., 17 *C.*, 2 *A.*
834—12 February, 1955, 11:30 a. m., to 12:00 noon, colony '55 B-IV with a sexual brood on the first statary day, 88 *C.*, 6 *A.*
944—2 March, 1955, 8:10 a. m., 6 *C.*
991—9 March, 1955, 10:45 to 11:45 a. m., taken within one meter of bivouac while colony had two columns out one to two meters, 8 *C.*
1170—16 February, 1956, 9:45 to 10:15 a. m., same raid as numbers 1171, 1172, 19 *C.*, 36 *A.*
1171—16 February, 1956, 10:15 to 10:30 a. m., 22 *C.*, 53 *A.*
1172—16 February, 1956, 10:30 to 10:45 a. m., 34 *C.*, 127 *A.*
1178—17 February, 1956, 10:15 to 10:30 a. m., 1 *S.*, 45 *C.*, 9 *A.*
1394—7 March, 1956, about 11:00 a. m., 1 *C.*
1411—8 March, 1956, 10:00 to 10:15 a. m., same raid as numbers 1412 to 1419, a large raid but not maximal, 7 *S.*, 16 *C.*, 7 *A.*
1412—8 March, 1956, 10:15 to 10:30 a. m., 4 *S.*, 15 *C.*, 14 *A.*
1413—8 March, 1956, 10:30 to 10:45 a. m., 6 *S.*, 31 *C.*, 37 *A.*
1414—8 March, 1956, 10:45 to 11:00 a. m., 7 *S.*, 49 *C.*, 32 *A.*
1415—8 March, 1956, 11:00 to 11:15 a. m., 6 *S.*, 13 *C.*, 24 *A.*
1416 to 1419—8 March, 1956, about 11:00 a. m., 2 *S.*, 2 *C.*
1569-A—26 March, 1956, about 10:10 a. m., 1 *C.*
1570—26 March, 1956, about 10:10 a. m., 1 *C.*
1574—27 March, 1956, 8:50 to 9:50 a. m., sweeping quite intermittently, 25 *C.*, 14 *A.*
1750—10 May, 1956, 4:20 to 4:30 p. m., swarm front very weak and never more than 20 cm. wide, 2 *C.*
1755—11 May, 1956, 9:25 to 9:40 a. m., same raid as 1756, 1 *S.*, 65 *C.*, 14 *A.*
1756—11 May, 1956, 9:40 to 10:10 a. m., aspirated as flies hovered over or sat within a few centimeters of cluster of ants around a cricket, 1 *C.*

1757—11 May, 1956, 1:50 to 2:05 p. m., same raid as 1758, 4 *S.*, 40 *C.*, 22 *A.*
1758—11 May, 1956, between 2:05 and 2:50 p. m., attempted to get more *Stylogaster* specimens and ignored *Calodexia,* 2 *S.*
1778—12 May, 1956, 6:00 to 6:30 a. m., 1 *C.*, only fly seen.
1782—13 May, 1956, 11:05 to 11:20 a. m., 58 *C.*, 23 *A.*
1784—14 May, 1956, 7:50 to 8:05 a. m., swarm front four to five meters wide, 19 *C.*, 17 *A.*
1790—15 May, 1956, 8:05 to 8:20 a. m., 1 *S.*, 27 *C.*, 20 *A.*
1849—25 May, 1956, 11:15 to 11:30 a. m., 2 *S.*, 79 *C.*, 9 *A.*
1854—26 May, 1956, 11:00 a. m., 5 *C.*
1860—28 May, 1956, 2:40 to 2:55 p. m., 4 *S.*, 38 *C.*, 3 *A.*
2191—26 July, 1956, 11:25 to 11:50 a. m., 33 *C.*, 1 *A.*
2230—30 July, 1956, between 9:45 and 11:45 a. m., 4 *S.*, 137 *C.*, 1 *A.*
2258-X—7 August, 1956, 10:45 to 10:55 a. m., 1 *S.*, 18 *C.*
2293—10 August, 1956, about 9:00 a. m., 7 *C.*
2302—11 August, 1956, 11:00 to 11:20 a. m., 1 *S.*, 101 *C.*
2329—17 August, 1956, 11:00 to 11:30 a. m., 56 *C.*
2331—17 August, 1956, 12:00 noon, 5 *C.*
2341—18 August, 1956, 9:00 to 10:00 a. m., 76 *C.*

Associated with Other Ants or Not Found Near Ants

995—10 March, 1955, 1:15 p. m., hovering next to bivouac of *E. hamatum*, 6 to 12 cm. over ants on ground next to bivouac, 2 *S.*
1552—22 March, 1956, taken in laboratory, 1 *C.*
1588-B—29 March, 1956, sweeping, not near ants, 1 *A.*
1666-B—21 April, 1956, sweeping, not near ants, 1 *A.*
1723—9 May, 1956, sweeping low vegetation in forest not near ants, 1 *C.*
1940—7 June, 1956, taken in laboratory, 1 *C.*
2110—9 July, 1956, 11:45 a. m. to 12:15 p. m., sweeping over swarm of workers of *E. vagans* which were milling around the site of a bivouac which I had disturbed. This colony had a brood of male and queen larvae, and the workers may have been more excited because of them. Workers covered the ground densely for only one-fourth to one-third square meter, with less dense ants over two square meters. By 12:15 p. m., when the ants had largely quieted down and retreated underground, most of the flies had disappeared, 3 *S.*, 18 *C.*
2216—29 July, 1956, sweeping low vegetation in forest not near ants, 1 *C.*
2236—Reared from cockroach into which larvae from adult fly were introduced through puncture in abdomen, 3 *C.*
2254-X—4 August, 1956, taken in laboratory, 1 *C.*
2260-X—7 August, 1956, 10:50 a. m., cricket taken escaping from swarm raid of *E. burchelli;* flies emerged 21 to 22 August, 8 *C.*
2346—19 August, 1956, 9:00 p. m., taken in laboratory, 1 *C.*

COMPARISONS BETWEEN FLIES ASSOCIATED WITH AMERICAN AND AFRICAN DORYLINES

The African doryline ants of the genus *Dorylus,* commonly known as the driver ants, also raid in large swarms and have many flies associated with their raids. No detailed study has ever been made

of the behavior or biology of these flies, but there are scattered observations indicating that some of the flies are strikingly similar to, and others quite different from, those associated with Neotropical army ants. As mentioned above, *Stylogaster* is also found accompanying the raids of *Dorylus*, but there are apparently no reports of its attacking cockroaches.

The conspicuous flies found with *Dorylus*, judging from the literature, all belong to the genus *Bengalia* (including *Ochromyia* of authors). This is a genus of Calliphoridae, but it is most unusual in that the adults are predaceous on a wide variety of insects. *Bengalia* apparently captures many of these insects in flight, but much of its prey is taken from *Dorylus* and other ants in raid columns. The most complete reports on this behavior are by Lamborn (1914, 1920), and his observations along with scattered reports by others have been reviewed by Bequaert (1922: 278-281). Although *Bengalia* usually has been reported as taking booty from the ants, it may also feed on the *Dorylus* brood, capturing larvae or pupae on emigrations. In addition, there is a report that the fly was seen to feed several times on the booty of an ant *without* carrying off the prey and *while* the ant remained holding the opposite end (Mellor, 1922). Like the flies with *Eciton*, *Bengalia* seems to find ant colonies by their odor. *Bengalia* is not known from the New World, and no flies with similar habits are known to be associated with Ecitonini.

Both the African and the American dorylines have large numbers of phorids living in the colonies. A few species of Sphaeroceridae (Borboridae, Cypselidae) have been described as myrmecophiles with *Dorylus* (Richards, 1951), but no information has been published on their behavior. In Panamá, we found a few sphaerocerids in refuse deposits of the ants and several species have been described from Brazilian dorylines. One species, *Homalomitra ecitonis* Borgmeier, was found in a column of *L. praedator*. [See Borgmeier (1955) for references.]

In addition, *Dorylus* and *Eciton* each has a myrmecophilous muscid which lays eggs over the columns. These eggs probably must be carried by the ants into the nests or refuse deposits in order to complete their development. This has been well substantiated for an undescribed species which we reared in Panamá, but the African evidence is based on only one observation of an ant carrying off an egg (Thorpe, 1942).

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An Application of Factor Analysis to Insect Behavior [1, 2]

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ABSTRACT: This study aims at demonstrating the value of multiple factor analysis in a dynamic biological model. Nineteen biological variables were taken from six species of insects. The variables were of two kinds: those involving pulsation of the heart or gut and those involving fleeing reactions when exposed on a glass surface. Six physical variables were measured concurrently with the biological variables. Fifty-five replicate readings were taken. Correlation coefficients were computed among the 25 biological and physical variables. These correlation coefficients were subjected to a complete centroid factor extraction and the results rotated to simple structure by the mass modification of Thurstone's analytical method.

Six factors appeared to cause most of the correlations observed in the study. Only one physical factor affects biological variables, namely, factor (I), the solar energy factor. Another physical factor (VI), which turned out to be a time series factor, did not affect any of the biological variables. The remaining four factors were primarily concerned with the flour moth (II), flour moth locomotion (III), the wasp (IV) and the louse (V). The effect of these factors

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on the 19 variables is discussed. The authors conclude that factor analysis is useful as a method of simplifying a correlation matrix into descriptive components called factors and that in suitable material at least some of these factors could be reified to meaningful physical and biological variables, while the unidentified factors serve to indicate the need for further inquiry.

I. INTRODUCTION

The present paper is an attempt to introduce a statistical technique, well known in the social sciences, to experimental entomology. It is to the best of our knowledge the first such application and consequently suffers from lack of refinement. As the analysis of the data progressed it became apparent to us that the choice of experimental variables had been unfortunate. The original aims of the study as detailed below could thus be only partially fulfilled. Nevertheless, we are convinced, and hope that the careful reader will agree, that our paper illustrates the potential value of the method. The authors have applied factor analysis to a series of different biological disciplines with moderate success, which they feel justifies continuation of such work. However, current research plans preclude a modified repetition of the present study in the near future. It was decided, therefore, to bring it before a biological audience in its present form in the hope that physiologists, ecologists and ethologists would find its method and philosophy of interest and might apply it in suitable instances.

a. Factor Analysis

Factor analysis is a method in some ways antithetical to the experimental method in science as practised in physics and chemistry and imitated with some success in the biological sciences. At least in its classical form factor analysis does not require the keeping constant or controlling of any one or several variables while the effect of yet another variable is being investigated. On the contrary, factor analysis permits the simultaneous variation of an entire domain of variables. It is designed to describe and analyze the simultaneous variation of a number of causes in a multiple cause-and-effect system. Factor analysis helps us in interpreting the simultaneous variation of a number of variables since ordinary graphic methods, even with the use of the perspective, are unable to depict more than the concurrent variation of three variables.

Factor analysis is a branch of multivariate statistics which in examining a complex set of phenomena attempts to express these in terms of a few underlying factors, which explain a large part of the variance of the original observations. A factor analysis always

starts with a table of intercorrelations among a number of variables. A number of different methods exist for analyzing these correlation coefficients into components represented by an k-dimensional vector space. The number of dimensions in this space corresponds to the number of major, common, varying factors which exist for the variables in the study and which may represent the causes of the correlations observed. Different techniques, some of them controversial, exist for resolving the correlation matrix into this so-called factor matrix, but space does not permit discussion of these details in the present paper. The interested reader is referred to the appropriate textbooks for a discussion of these points (see Cattell, 1952; Fruchter, 1954; Thompson, 1951; Thurstone, 1947).

The result of such a factor extraction is a so-called factor (F_o) matrix which represents the correlations of the variables with the k factors. Each table consists of a column of loadings for each factor, which represent the magnitude of the effect of the factor on each of the variables in the study. By suitable manipulation of these data the original correlation matrix can be reconstituted from the F_o matrix. It should also be pointed out that the factors in an F_o matrix are themselves deliberately uncorrelated. The F_o matrix can then be rotated by a series of computational steps into a different matrix known as the simple structure matrix, which represents correlations of the variables with new factors known as reference vectors or simple axes. The simple structure concept is a controversial one in factor analysis and it is not our intention to enter upon this controversy here. Some of the problems involved are discussed in a technical companion paper (Sokal, Daly & Rohlf, 1961). Suffice it to say that we hoped that our data would exhibit simple structure and we therefore rotated our data to the simple structure position. By simple structure is meant a situation where each factor affects only a few of the variables in the study and each variable is affected by only a few of the factors. In the simple structure constellation reference vectors themselves are permitted to be correlated and we are therefore left with a system of possibly correlated causes.

For the purposes of describing a complex situation it is best to have a series of causes and associated regression coefficients which show the effect of each cause on a particular variable. Since the simple structure matrix is a matrix of *correlations* between causes and variables, it is best to change this matrix for final presentation (as was done here) into a so-called primary pattern matrix which shows factors or primary axes and their loadings on the variables of

the study. The loadings are analogous to standard partial regression coefficients. A primary pattern matrix is usually reproduced as the final result of a factor analysis and we show such a matrix in table 3 of our paper. It can also be represented as an arrow diagram, a simplified version of which is shown in figure 4 of our paper.

The basic philosophy of factor analysis is the assumption that the correlations among the various response variables are based upon the effects of few so-called factors. The factors which emerge from such a study are hypothetical constructs which can frequently be shown to possess objective reality, either through reappearance in successive factor analysis of similar material (invariance) or by positive identification as known causal factors. Even if these are not causal variables in the generally accepted sense, they are at least acceptable indicators of the moving forces in the complex situation represented by the correlation matrix. We can therefore employ factor analysis with profit when (1) the underlying causes are unknown; (2) the underlying causes cannot be controlled; or (3) when the very nature of the research problem makes control of causal factors undesirable.

Factor analysis has been used extensively in the field of psychology where it was first discovered and developed. It also has some application in the fields of education, sociology and economics. Its application to the biological sciences has been relatively rare and recent and instances of its employment can be limited almost entirely to the analysis of morphological correlations. In psychology and the social sciences the discovery of true causal factors is intrinsically very difficult and several generations of scientific research may yet have to pass before the so-called psychological factors can be reified to any appreciable degree. Some hope remains, however, that in appropriate fields of the biological sciences the causal variables obtained by factor analytic methods might be identified with known or discoverable biological factors. By this means a method might be included in the investigational repertoire of the biological scientist which might complement, or in certain cases replace, the traditional experimental analysis.

b. Possible Application in Biology

From what has been said above it appears clear that factor analysis can be employed whenever a correlation matrix can be computed among a number of variables. We may follow Cattell (1952) in distinguishing between P, Q, and R type matrices. The latter are the ordinary correlation matrices in which N subjects are studied

for a series of n variables; *i. e.*, a reading is taken on each subject for all n variables. The correlations are computed among the n variables. A related technique, studied on only one subject, is the P technique, in which n variables are correlated but over a period of N times for the same individual. The Q technique refers to correlations among the N subjects based on the n characters. Thus a Q type matrix is of dimension $N \times N$.

All three matrices have obvious and significant biological applications. The R type matrix may reveal causes for correlations among characters. These could be physical or physiological factors producing the correlation of certain physiological or morphological characters, or they could be evolutionary factors if the correlation of a number of characters is studied over N different species within a genus. A number of studies of the former type have been performed, such as the study of Howells (1953) on body types in man and similar studies by Hammond (1957). The second type of study, investigating evolutionary factors within a taxonomic group has been carried out by Stroud (1953).

The writers are not aware of a P type factor analysis in the biological sciences, although such a study should have great merit in a physiological analysis where the study of a number of individuals might be difficult, but where several characters of a single individual can be studied over a considerable period of time. A second application of a P type study would be the observation of a population or other supraindividual entity over a period of time. A Q type study can aid mostly in problems of classification and such a study has been undertaken by the senior author (Sokal 1958a) on a group of four genera of bees.

As will be shown by the experimental work below, it can be quite profitable to combine experimental work with factor analysis in cases where some factors cannot be controlled easily, or where it is undesirable to control such factors. On the other hand there are a number of situations in biology where the experimental method is singularly unsuited to an explanation of the causal relationships involved. We refer to ecological studies in the field where a variety of factors exist in complicated interrelationships. It would be quite difficult to control any one of the component factors in the field but it would be relatively easy to measure the responses of given animals or populations under the freely varying conditions. Factor analysis might serve at least as a first exploratory tool in describing the causal variable acting upon the population and might very easily lead the

investigator to search for and identify significant causal components of the environment.

c. Specific Aims of This Study

The present investigations had a number of specific aims which can be broadly classified into two groups. The first group has to do with a demonstration of the value of factor analysis as an analytical tool in biological experimentation. The second aim pertained to a number of points in factor analytic theory and practice which are largely beyond the scope of the present paper and which are reported in a special publication for the benefit of workers specializing in the field (see Sokal, Daly & Rohlf, 1961).

For the purposes of this paper it was important to find a series of physiological or behavioral variables in a number of insects which could be studied relatively easily in the laboratory and which could be related to few (three) environmental causal variables. From the point of view of the analysis it would have been ideal if the data would have exhibited simple structure as enunciated by the Thurstone school of factor analysis (see Fruchter, 1954, page 110 for a simple explanation of this concept). We would therefore have preferred that each variable be affected by no more than two of the three factors and that each factor affect no more than a very few of the response variables. With the limitations of the animal material and equipment available in our laboratory it soon became obvious to us that this ideal situation could not be produced. We therefore had to settle for a series of characters the causation of which could only be guessed at. It was hoped that temperature, light and relative humidity, the three "causal" variables which were measured and recorded, would produce some effect roughly similar to that of simple structure in the response variables. In this we were only partially successful.

As will be seen below a very satisfactory simple structure was obtained. However, the response variables were only partially affected by the "causal" variables. When the data were analyzed it became apparent that much of the covariation and correlation in the study was due to factors which were either species specific or situation specific. This in no way detracts from the intrinsic value of factor analysis as an analytical tool. However, it does weaken the demonstrative value of the present study.

We had hoped to show by our analysis that the correlations yielded factors which were already well known to the experimenter

and which therefore would corroborate his previous findings. Such an outcome of our study might have convinced our readers that factor analysis could be of analytical and predictive value also in cases where the causal situation was not known. Unfortunately, it turned out that the common causes responsible for the correlations among our variables were partly within the realm of the unknown. In this particular study we are thus only slightly better off than are the human psychologists who have used factor analysis to describe the simpler and fewer dimensions of the human mind which they believe responsible for the complexities of performance in a series of achievement tests, but which they have been unable to reify.

Our actual experimental plan was the following: we decided to study 19 different behavioral responses of six species of insects in the span of one to two hours. These observational periods were repeated, sometimes at daily intervals, sometimes two or three readings per day, until a total of 55 observations of all 19 characters had been accrued. The entire study lasted for twenty-two days starting on the 10th of September 1957. Together with the reading of the 19 response variables on the insects, six readings were taken which might conceivably be related to the true causal variables of the study. These six readings represent temperature, light, relative humidity, pressure, hour of the day and number of days of the study. The correlation coefficients which were computed were correlations among the 19 response variables and six "causal" variables over the 55 replications of the experiment. It was hoped that the factors which could be extracted from a correlation matrix of these 25 variables would in some measure reflect common causes and would also demonstrate that at least some of the six "causal" variables were really common causes producing the correlations observed in the other 19 variables.

II. MATERIALS AND PROCEDURES

Table 1 contains a summary of biological materials and the procedures employed in the study. The reader may find it helpful to refer to this table while using this section. The species selected for the study were those conveniently available in the various laboratories of the Entomology Department at the time. The first column of table 1 presents the scientific as well as common names of the six species employed.

A program was designed to record the performance of each species for each replication as follows: After the individuals were collected from the cultures and brought to the test room (fig. 1), one of each

TABLE 1.—Summary of Materials and Methods Used in the Experiment

NAME	Source	Rearing method	Culture room temperature*	Type of individuals used	Sequence of testing	Name of response variable	Response variable code number
Periplaneta americana L. (American roach)	Captured on campus of University of Kansas	100 adults per cloth covered 18-inch cube cage; water, dog biscuit, banana and lettuce.	23° C.	Adults of unknown sex or age	1	Heart Beat	1
Pediculus humanus L. (Human louse)	University of Kansas culture.	On felt pads in finger bowls; fed to satiation on rabbit once each day.	30° C.	Adults or large nymphs of unknown sex or age with gut partly filled with darkened meal.	2 6 6 6	Gut Beat Rate of locomotion Angle to light Excursion index	2 8 9 17
Tribolium confusum Duval (Confused flour beetle)	University of Minnesota culture.	50 adults to 200 grams whole wheat flour in ½ pint milk bottle.	23° C.	Adults of unknown sex or age.	4 4 4	Rate of locomotion Angle to light Excursion index	4 5 15
Ephestia kuhniella Zeller (Mediterranean flour moth)	North Carolina State College culture.	Oviposition of about 40 adults in cardboard box of yellow corn meal, more meal added at later intervals.	23° C.	Larvae about 1 cm. long of unknown sex or age.	3 7 7 7 7	Heart Beat Rate of locomotion Angle to light Undulation rate Excursion index	3 10 11 12 18
Habrobracon juglandis (Ashmead) (Parasitic wasp)	North Carolina State College culture, strain No. 33, Wild type.	Oviposition of two females for two days on five *Ephestia* larvae in vial plugged with cotton.	30° C.	Adult females no more than five days since ecdysis.	5 5 5	Rate of locomotion Angle to light Excursion index	6 7 16
Musca domestica L. (Housefly)	University of Kansas culture, brother-sister inbred for 10 generations.	About 100 eggs per ½ pint milk bottle of CSMA medium.	30° C.	Larvae five days old of unknown sex.	8 8 8	Rate of locomotion Angle to light Excursion index	13 14 19

* The 30° C. cultures were controlled, the 23° C. were subterranean rooms without controlled temperature; there were no humidity controls.

of the species except the roach was placed in its own small glass vial painted dull black and covered with nylon mesh. The roach was immobilized on a piece of glass with narrow strips of clear cellulose tape over the outspread wings and the abdomen. One additional *Ephestia* moth larva was taped across the dorsum onto a microscope slide with cellulose tape. One additional louse was put down onto the sticky side of a loop of tape placed on a microscope slide. All the insects were now put into a cardboard box painted dull black. This box was constructed to admit a current of air from a fan, and to exclude measurable light by a series of baffles. After at least one hour, the lid was removed. At intervals during the performances, the diffuse light (23)* was measured in foot-candles with a Weston illumination meter, temperature (20) in degrees Fahrenheit read from an alcohol thermometer, and relative humidity (21) computed with a companion wet-bulb thermometer. Pressure (22) was taken later from a recording barograph located at the U. S. Geological Survey office at the University. An average of the readings for temperature, and humidity was used as indicative of the environmental conditions during the hour of testing. The range in temperature per experimental period averaged $1.44 \pm 0.278°$ F., while the range in relative humidity averaged $3.3 \pm 0.50\%$. Separate light readings for each insect performance were used in the analysis, since these varied widely in a period. Day of the experiment (24) and hour of the day when the experiment was run (25) were two variables available as by-products of the experimental setup and were included in the correlation matrix.

The testing stage faced the open window of the room (see Fig. 1) and was surrounded on the other three sides by a foot-high wall painted dull black. On this horizontal stage was placed a pane of frosted glass. The insects were tested in a standard sequence which can be learned from column 6 of Table 1. The three insects immobilized on slides were tested first. They were oriented with head toward light and were observed with a low power binocular microscope placed on the stage. The pulsations of the dorsal vessel (1) of the roach were counted by hand tally three consecutive times for one minute each. The average of the three readings was used. The peristaltic waves of the midgut (2) in the louse were similarly counted and the average per minute computed. Finally, the counts of pulsations of the dorsal vessel (3) of the moth larva were averaged.

* Variables, both "causal" and response are identified by numbers 1 through 25. Numbers 1-19 are response variables, 20 through 25 "causal" variables.

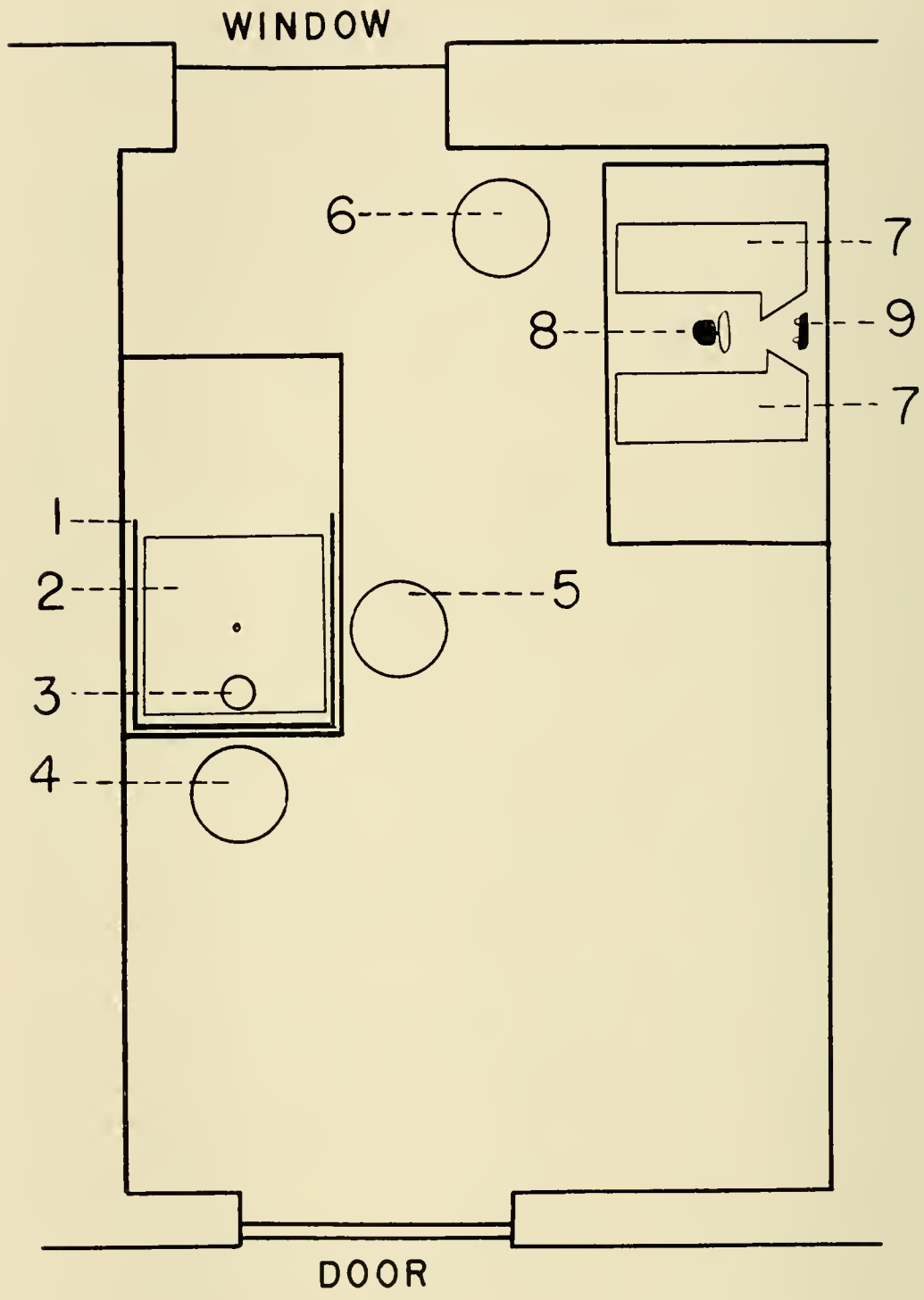

FIGURE 1. Diagram of the room in which the experiments were performed. The window faces south with the sky obscured on the southeast by a portion of the building. During the experimental periods, the casement window was open, the door shut, and all artificial light was absent. Only diffuse light reached the insects from the window and from the reflection of the pale colored walls of the room. (1) is the black wall around the stage (2) with its central release point; (3) is the site of the readings for light and the position of the microscope when in use; (4) is the position of the experimenter when using the microscope and (5) was his position when the routes were traced; (6) was the position of the assistant; (7) is the cardboard container which admitted a current of air from the fan (8), but excluded light; (9) is the position of the thermometers.

The next four insects (from the vials) were, in turn, allowed to run across the level frosted glass plate from a standard central mark. The granular surface gave sufficient friction for their locomotion. If the insect failed to fall from its vial with moderate shaking, it was teased out with a brush. Immediately a clear pane of glass was poised ¼ inch above the frosted pane by dull black wood blocks at the corners and aligned with the frosted pane by standard marks on each. As the insect began to move, a stopwatch was started by an assistant and the track of the insect followed on the upper pane in washable ink. At equal periods of time, the assistant signaled and the tracer made a small additional mark on the track. As soon as the insect has attained the margin of the glass, or when the testing period had exceeded five minutes, the tracing pane was removed and the insect destroyed. For each of the four insects a separate tracing pane was used. Finally, the larva of the housefly was taken from its vial onto the frosted pane and a small drop of methylene blue solution (3 grams to one liter distilled water) was placed on the caudal end of the larva with a small syringe and 26B-D needle. Locomotion on the glass was facilitated by the liquid and the track stained with the dye. At the end of each minute, an additional drop was added while the larva crawled and a small mark made on the track. As before, the insect was destroyed after the trial. Ten tracks were less than 5 cm. and were discarded because they were inadequate for measurement. The remainder were traced onto large sheets of white paper. A typical tracing is reproduced in figure 2. On these tracks, the distance between time marks was measured with a map measurer and an average rate of locomotion computed in centimeters per minute for the whole track. Additional marks were placed on the track at 5 cm. intervals. A ratio was computed of the linear distance from the start to the last 5 cm. mark. divided by the total distance of the insect's journey to that mark. This ratio, which we called the excursion index, was near unity for insects moving in a straight line, less than unity for deviations from linearity. A line was now drawn across the map perpendicular to the source of light (the window). The 5 cm. marks were connected by straight lines. The angles between each of these straightened segments of the track and the line representing the direction of the light were taken and an average angle to light computed for the track. For insects attracted to light the acute angle was measured while for those moving away, the obtuse angle was recorded. An additional variable, the number of locomotory undulations (12), was recorded for the moth larva.

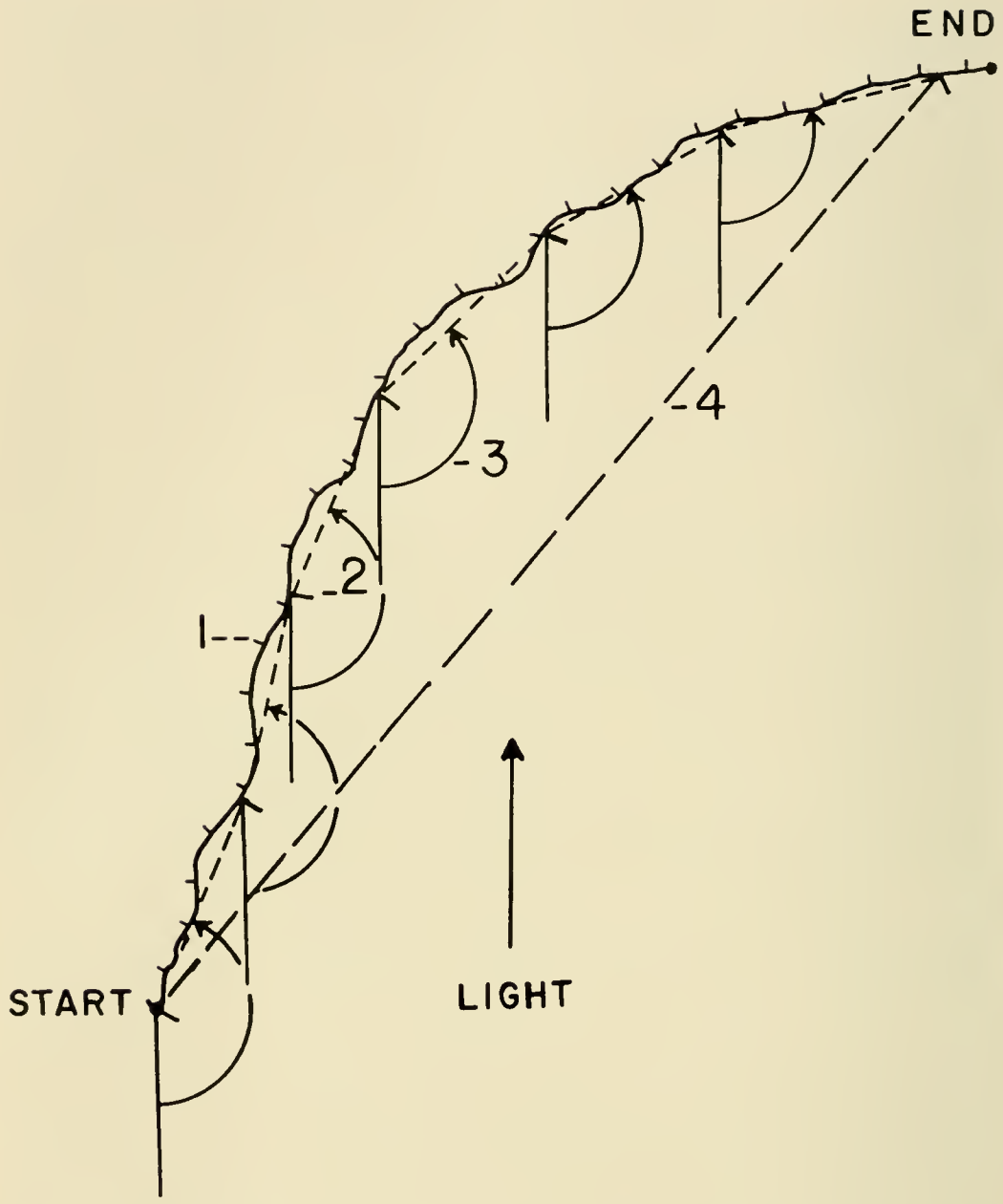

FIGURE 2. Diagram of an insect's track with the additional marks used in determining the rate, angle, and excursion index. (1) is a time mark; (2) is a 5 cm. mark; (3) is the angle measured for the straightened segments of the track; and (4) is the linear distance involved in the excursion index.

After the readings had been obtained the next step was the computation of the correlation matrix. Some of the variables had to be transformed in order to approximate normal frequency distributions which are required for the Pearsonian product-moment correlation coefficient. The frequency distributions and their transformations are shown in figure 3. Transformations such as square root and probit were used. For details of this aspect of the procedure the reader is referred to the companion paper (Sokal, Daly, & Rohlf, 1961). A second problem was the absence of readings for certain

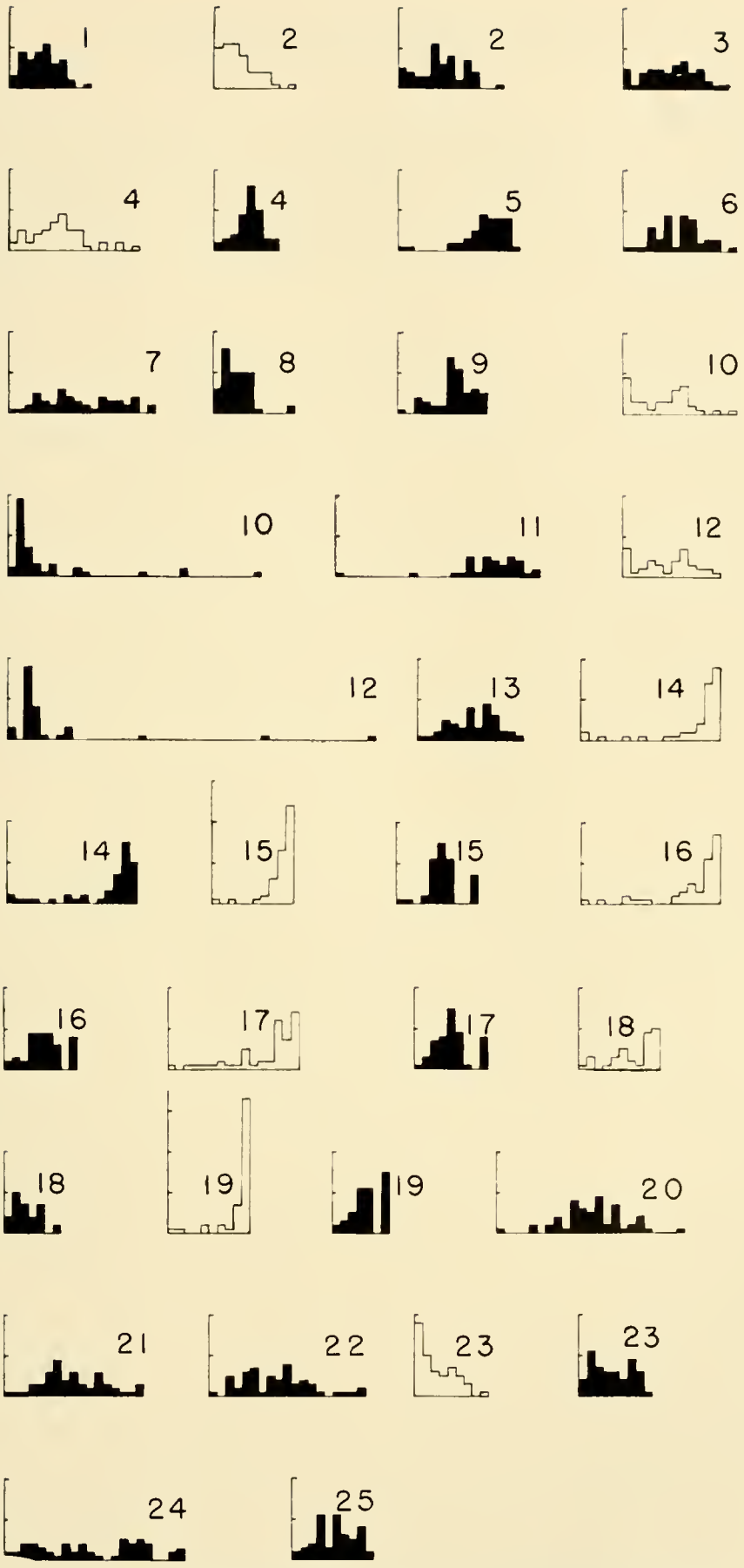

FIGURE 3. Histograms of the variables. Black histograms are data as used in the analysis. Clear histograms are data before transformation. Units of the ordinate represent 10 units of frequency. The numbers next to the histograms refer to the code numbers of the variables given in table 1 and in the text.

variables during some replications. Such missing observations could result from several different situations. In some cases the animal refused to move appreciably when placed on the glass plate under the experimental situation. A few readings were not obtained either by oversight or were not used if the recorded readings were obviously in error.

The computation of the correlation coefficient was by the customary procedure, except that the missing readings necessitated a special program which took into account the varying sample sizes encountered for the different correlation coefficients. The actual computation was carried out on the University's IBM 650 digital computer. While the computational task was considerable it should be pointed out that it was not beyond the capability of a desk calculator operator. The question is entirely one of time. The computation on the digital computer took approximately one and a half hours while it would have taken a desk calculator operator two to three weeks to perform the same computation.

III. RESULTS AND DISCUSSION

a. The Correlation Matrix

The matrix of correlation coefficients among the 25 variables computed as described above is shown in table 2. Significant correlation coefficients are shown in italics. It may be seen that only 44 out of the 300 possible correlation coefficients are statistically significant at the 5% level. While this is a disappointingly low figure it is nevertheless three times what may be expected from chance sampling alone and there is little question that the significant correlations are real. The over-all level of the correlations is quite low and the average absolute correlation is 0.15. This feature of the experiment was somewhat disappointing to us since we had expected to find a greater amount of covariation in our data, which would have lent more meaning to the final analysis and have given us higher factor loadings in our final factor matrix. The reasons for the low correlations are several. We may suppose that, regrettably, the variables chosen by us were not such as to be highly correlated under the circumstances under which they were studied. A person acquainted with literature in insect physiology may wonder why correlations between physical environmental factors and some physiological response variables shown in our study were not as high as those published in the literature. The reason for this seems to be that our material was heterogeneous with respect to

TABLE 2.—Matrix of Correlation coefficients among the 19 response and 6 "causal" variables. Coefficients significant at $P \leqslant .05$ are in italics. Code numbers for the variables are explained in table 1. Decimal points in front of the coefficients have been omitted here and in tables 3 and 4 below.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
2	*39*																								
3	*28*	22																							
4	04	−08	26																						
5	08	−16	16	−10																					
6	*36*	06	18	*28*	−04																				
7	−08	−10	14	−02	02	07																			
8	*33*	*34*	14	−21	21	09	02																		
9	−14	01	*−36*	−03	22	−06	−06	10																	
10	06	09	15	−12	−04	02	04	−04	−12																
11	12	*38*	−22	−13	−23	13	−05	−12	−01	00															
12	−23	13	−03	−19	04	*−36*	10	26	19	50	−09														
13	14	16	15	18	−05	00	−17	−04	12	−08	−03	−13													
14	−05	−08	−04	−15	07	03	05	−01	−17	24	01	*45*	−09												
15	−16	−08	−08	−13	21	−05	11	*31*	22	−12	07	06	−02	−10											
16	10	−20	02	20	−22	*41*	19	01	−16	−25	−19	*−39*	−28	18	*−32*										
17	−02	07	−26	−23	*29*	−17	−08	*34*	59	17	10	39	−06	−18	32	−11									
18	−02	05	*−38*	06	−22	17	01	−02	−06	−20	29	*−42*	24	−04	16	08	−20								
19	−22	−20	−21	−02	−23	03	06	−18	02	−14	14	−13	18	06	−10	−12	−01	10							
20	*67*	*48*	*32*	11	−01	34	−08	*32*	00	−10	19	−11	*28*	−14	−25	18	−11	02	−11						
21	*−41*	−21	−23	01	04	−04	06	−20	08	−09	−05	08	−16	18	16	01	09	−10	15	*−66*					
22	04	−08	−23	−08	−07	−04	−03	14	06	−20	28	−20	10	−09	11	−15	05	26	05	05	*−40*				
23	*44*	10	*32*	*29*	02	*34*	−03	08	−08	29	−10	03	*30*	−09	−20	01	−13	06	−10	*51*	*−62*	18			
24	−08	−06	−10	−24	−15	−19	22	13	08	03	08	05	13	−15	00	−24	02	−05	20	05	*−41*	*60*	*28*		
25	*40*	23	*27*	*34*	−03	25	−31	16	−20	−09	−16	−04	25	−13	−25	20	01	−03	−15	*50*	−26	−15	27	−18	

age, sex, physiological condition and genetic background. We were thus not able to observe it under the carefully controlled conditions which are customary in investigations in insect physiology. On the other hand, these uncontrolled conditions had desirable aspects for our study since they simulated the kind of variations in response which can be observed under natural conditions. The fact that the physical variables were not independent of one another would tend to lower the correlations. For instance, under our experimental setup temperature was not varied independently of relative humidity and in general changes in temperature brought about correlated changes in relative humidity. It might well be that such variables as roach heartbeat and louse gutbeat, when subjected to changes in temperature under constant relative humidity or a constant saturation deficit, might have yielded higher correlations with temperature than they did.

b. Summary of Factor Analytic Procedures

Factor analysis is sufficiently complex so that it would be futile to expect the statistically uninitiated reader to follow its technical arguments. Such readers will have to be satisfied with an understanding of the final results arrived at by this method. Those readers with a sufficient background in statistics may wish to learn and understand the specific computational steps which are involved in this method. However, it would be impossible within the space allotted to this paper to present the methods and the reader is therefore referred to the available series of textbooks in this field. The authors can recommend particularly Fruchter (1954) as a source of simple computational procedures and Cattell (1952) to provide the philosophical background of the method. It is necessary at this place only to make a brief statement for the record of types of computations undertaken leaving all explanation of these to the reference sources indicated.

The correlation matrix was subjected to a series of different factor analyses which are described in greater detail in the companion paper (Sokal, Daly & Rohlf, 1961). As can be found in that publication the various types of analysis gave surprisingly concordant results and it was therefore decided that the final analysis involving the study of 25 variables (19 response variables and 6 "causal" variables) would be the most meaningful one. This correlation matrix had its factors extracted by Thurstone's complete centroid method and communalities were stabilized by a series

of iterative extractions. We were able to extract six common factors. The resultant F_0 matrix was rotated to simple structure by the semi-analytical method of Thurstone as modified by Sokal (1958a). The simple structure matrix which resulted from this procedure was converted by the conventional formulae to a primary pattern matrix.

c. Results of Factor Analysis

The variables and their loadings. Table 3 shows the primary pattern matrix for the six factors and 25 variables. Such a matrix

TABLE 3.—Primary pattern matrix showing effects of six factors (primary axes) on the 25 variables of table 2.

VARIABLES	Factors					
	I	II	III	IV	V	VI
1	77	05	−05	15	04	−03
2	65	36	22	−21	09	−17
3	24	−62	05	−07	−35	−01
4	09	−25	−34	06	−26	−12
5	−11	−48	−02	−04	34	−05
6	40	07	−25	50	−04	−11
7	−13	−12	06	33	−01	22
8	42	−04	12	12	45	07
9	−06	11	−05	−03	58	04
10	15	−01	61	−09	−18	08
11	29	67	03	01	−14	01
12	00	−02	96	−29	05	−02
13	22	07	−15	−32	−14	09
14	−05	13	50	14	−24	−12
15	−21	−08	−11	−04	50	02
16	07	03	−34	94	−06	−15
17	10	11	18	−09	79	−01
18	06	43	−35	09	05	03
19	−21	26	−06	−05	−15	15
20	98	22	01	07	−04	07
21	−64	01	02	08	08	−54
22	11	18	−25	−01	22	64
23	56	−17	01	05	−24	41
24	03	−01	08	−14	02	84
25	51	−07	−18	−06	−16	−27

indicates the magnitude of the effects (loadings) of the factors on the variables. The larger the loading of a given factor on a variable the greater will be the effect on the variable. These loadings are analogous to standard partial regression coefficients and can under certain conditions be larger than unity although none of the values in table 3 are of such magnitude.

Table 4 shows the correlations among the 6 factors (primary

TABLE 4.—Correlations among factors (primary axes) of table 3.

FACTORS	Factors					
	I	II	III	IV	V	VI
I						
II	-30					
III	-09	-14				
IV	-08	-07	22			
V	-02	-13	15	-09		
VI	-07	13	00	01	-01	

axes). It can be seen that none of these correlations exceeds .30 in magnitude and most of them are very small indeed. For our purposes, therefore, the factors which appear to exhibit simple structure are essentially uncorrelated with each other. This greatly simplifies the interpretational picture. In all further discussion correlation among the factors is therefore ignored.

Since there is no method established to test the significance of factor loadings we have arbitrarily selected a level of .4 as the lower limit of important factor loadings. In other words we will be concerned with the biological interpretation of loadings equal to or greater than .4. A diagram (fig. 4) of the factors and variables was constructed based on the .4 criterion of importance. When this scheme is adopted four of the variables (4, 7, 13 and 19) are omitted from the diagram since they are not affected to the extent of .4 by any of the common factors obtained by the factor analysis. This is not surprising because an inspection of the communalities of these variables (the amount of variation which they share with other variables) reveals that they are very low in every case (all lower than .27). It may therefore be expected that these variables have no common factor in the study. The reasons for their variation are obscure and presumably differ from variable to variable.

The discussion of the results of the factor analysis which ensues will be organized in the following manner: We shall first discuss the individual variables, grouped by species rather than in their numerical order and followed by the physical, "causal" variables. The variables will be discussed from two points of view. We shall discuss their range and their variation making reference to figure 3 and also discuss the factors affecting them, making reference to figure 4 and to table 3. After a discussion of the variables we shall

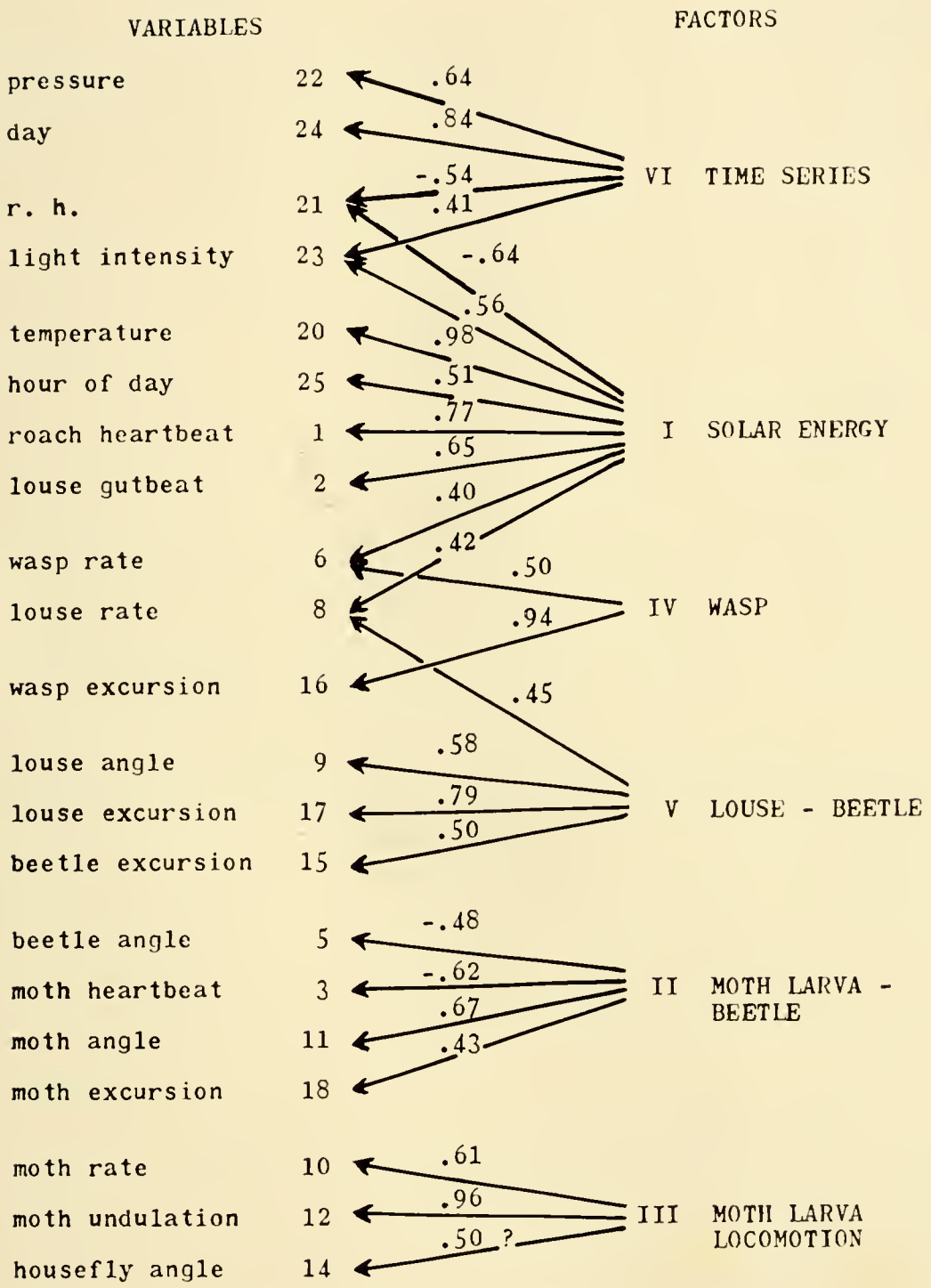

FIGURE 4. Arrow diagram showing important ($\geq .4$) effects of factors on variables. Data for this graph have been taken from table 3. Correlations among factors (primary axes) are not shown since they were quite low (see table 4).

summarize the nature of the covariation in the study by a discussion of the factors.

The heart beat of the roach (1) varied from 65 beats per minute to 155 beats per minute in a reasonable approximation to normality, although some evidence of bimodality might be detected. The variable was not transformed. It appears to be affected only by factor I which, as will be seen later, seems to be the factor representing the general energy level of the environment. This is a reasonable relationship based on the knowledge of this character from previous studies (Beard, 1953). The rate of heart beat was doubtlessly affected by the immobilization of the roach and its resultant struggles for freedom.

In looking over the louse characters we find that gutbeat (2) varied from 4.5 beats per minute to 58.5 beats per minute and was considerably skewed to the right. A square root transformation when adopted spread the data out considerably, although it still could not be considered to have produced the normal frequency distribution. Gutbeat is affected by factor I, the energy factor, which again reflects the increase of metabolic activity with an increase of temperature. This relationship was probably lowered by the fact that the louse was tethered and also since there was variation among individuals in the extent of the inflation of the gut. The rate of locomotion (8) of the louse varied from 1 cm. per minute to 19 cm. per minute, with some indication of a skew to the right. The data were not transformed. The rate of locomotion is affected by the energy factor (I) as well as by factor V which influences mostly the louse, but also one aspect of our beetle behavior. An increase in factor V appears to raise the rate of locomotion of the louse.

The louse's angle to light (9) varied from 76 degrees to 176 degrees. Only one louse reacted at less than 90 degrees which means that essentially all were repelled by light. Of all the insects studied the lice had the most circuitous path as will be seen in the excursion index. The data were not transformed. The distribution of the excursion index in the louse (17), like that of all the other excursion indices in the study, is strongly skewed to the left. The excursion index really represents a percentage. It was found, therefore, that the probit transformation gave an adequate transformation for this as well as all other excursion indexes. The range in values was from .23 to .98. Both the angle to light as well as the excursion index are positively affected by factor V. We may therefore summarize the relations of the louse variables in the following manner:

gutbeat and the rate of locomotion both appear to be affected by the energy factor (I). It should be noted that the effect of factor I on the louse emerged, although variables (2) and (8) were measured on different individuals. Rate of locomotion is also affected by factor V, which factor will make the louse not only move faster, but also move away from the light and along a more direct path.

Only three flour beetle variables were measured. The rate of locomotion (4) was skewed to the right and ranged from 3 to 78 cm. per minute. A square root transformation managed to make the data more bell shaped. Flour beetle rate was one of those characters that did not possess more than a minute amount of variance shared with other variables and therefore no common factor appears to have a high loading on it. We have to conclude that some unknown cause, unrelated to the physical variables measured by us, affected the locomotory rate. The range of temperatures offered, which varied principally from 72° F. to 84° F., did not affect the rate of locomotion. The angles to light (5) varied from 36 degrees to 176 degrees, but this range is misleading since all but two of the animals exhibited an angle of larger than 90 degrees toward light, showing that the beetles were negatively phototactic. The data were not transformed. The excursion index of the flour beetle (15) was relatively high showing approximate straight line movement by the beetle. The index ranged from .05 to .95 but with most data massed between .75 and .95. It was transformed by the probit transformation. When discussing the effect of factors on (5) and (15) we are faced with a situation which is very difficult to interpret. There appears to be no common factor at all affecting flour beetle variables. Variable (5) is negatively affected by factor II, while variable (15) is positively affected by factor V. Factors II and V seem to be responsible largely for flour moth and louse variables, respectively, and the relations of these factors to the flour beetle are obscure.

The five variables measured on the flour moth larva fall into two distinct groups owing to their relations with common factors. The rate of locomotion (10) and the number of undulations per minute (12) were both affected by factor III. The heartbeat (3), angle to light (11) and excursion index (18) were affected by factor II. The rate of locomotion ranged from 1 cm. to 27 cm. per minute. The frequency distribution was skewed to the right as well as bimodal. Transformation to the square root of the reciprocal of the rate provided a somewhat more acceptable frequency distribution. The number of undulations per minute had a distribution similar to that of the previous variable. It ranged from 5 to 115 undulations per

minute. The same transformation was employed. Factor III has extremely high loadings on the number of undulations and moderately high loadings on the rate of locomotion. It appears that this factor is none other than the rate of undulations itself. It is fairly obvious that the rate of locomotion will depend very largely on the undulation rate. It is interesting to note that this relation is not a perfect one, *i. e.*, that there must be factors other than the number of undulations determining rate of locomotion. What caused differences in undulation rate we cannot learn, except to say that it does not appear to be related to any of the other factors in the study.

The heartbeat of the flour moth larva ranged from 6 to 126 per minute and was reasonably evenly dispersed over the various frequency classes. The variable was not transformed. Angle to light ranged from 53 to 173 degrees with, however, all but one reading 98 degrees or larger. The readings were evenly dispersed and the data were not transformed. The excursion index of the flour moth larva ranged from .53 to .98 and was transformed by the use of probits. All three variables are affected by factor II. This factor appears to reduce the heartbeat of the flour moth at the same time making it go straighter and farther away from the light. It should be pointed out that the heartbeat was measured on a different individual from that which performed on the glass plate. An interpretation of these findings is given in the discussion of factor II below.

Three wasp characters were measured. The rate of locomotion of the wasps (6) ranged from 13 centimeters per minute to 78 centimeters per minute. It was somewhat bimodal but was not transformed. The rate of locomotion was affected by factor I, the general energy factor, as well as by a special wasp direction factor (factor IV), which will be discussed later. Variable 7, the angle to light of the wasp, was one of the variables having no correlations whatsoever with any other ones and therefore exhibiting no common variance. It ranged from 6° to 176° and was randomly distributed to each side of 90°. We may therefore state that the reaction of *Habrobracon* to direction of light was essentially random. Whatever factors did determine this response were not apparent from our study and did not seem to affect any of the other variables. The excursion index ranged from .18 to .98 and was transformed by the probit transformation. It is affected very highly (.94) by factor IV which appears to be a directed movement factor in the wasp.

In the housefly larva we studied rate of locomotion (13) which ranged from .8 cm. to 18.8 cm. per minute in a more or less bell

shaped fashion. This particular variable had no common variance as did variable 19, the excursion index of the housefly larva, which ranged from .53 to .98. Variable 14, the angle to light of the housefly larva, ranged from 6° to 176° with most readings in the range above 90°. Its distribution was extremely skewed to the left, most larvae maintaining an angle of 166° or more with the light. Successive trials at transformation failed to remove this skewness to our satisfaction. The final transformation adopted, the reciprocal of the square, while better than the original scale, was still not adequate. It appears that the very skewness of the variable biased the computation of the correlation coefficients in such a manner as to produce spurious correlations. While other housefly variables did not exhibit the effects of common factors, the angle to light was affected by factor III, which otherwise appears to be a moth larva undulation factor. When the moth variables were studied in connection with variable 14, it could be shown that the resulting scattergram reinforced the bias of the two non-normal distributions. We believe therefore that the effect of factor III on the housefly angle to light is spurious.

The physical, so-called causal, variables were the following: temperature (20) ranged from 66° F. to 88° F.; most of the temperature readings lay between 72° F. and 83° F. The distribution was reasonably bell shaped and no transformation was attempted. Temperature is strongly affected by factor I, the solar energy factor. Relative humidity ranged from 28% to 76%, with a distribution similar to that of temperature. The data were not transformed. Relative humidity was affected both by the solar energy factor (I) and the time series factor (VI). Pressure ranged from 28.82 to 29.36 inches. While the distribution was anything but normal it was of such indefinite shape that transformation was not attempted.

A separate series of light readings had to be taken for each variable as was explained in the Materials and Procedures section. Nearly all light intensities ranged from 25 to 475 footcandles, were strongly skewed to the right and truncated at the left with an accumulation of values at the lower end of the scale. A square root transformation of the data improved the appearance of the frequency distribution but generally accentuated a tendency toward bimodality which was present in the data. This bimodality may have been induced by passing clouds. Light was affected both by

the solar energy factor (I) and by the time series factor (VI). The day of the month (24) was more or less evenly distributed over the 21 days with an average of three readings per day. The hours of the day (25) ranged from 0800 to 1800 hours and showed peaks just before 1200 and just after 1300 hours. The last two variables were not transformed since they could not be expected to have normal distributions.

We shall now summarize the effects of the individual factors and speculate upon their nature.

The factors. The physical factors will be discussed first followed by the apparently biological factors. The numerical code of the factors is entirely arbitrary when first assigned, but in order to make the factors consistent with a factor analysis of the sub-matrices (see Sokal, Daly & Rohlf, 1961) we adopted the system given here. Factors are therefore not necessarily discussed in numerical order.

Factor I is most probably an indication of the variation in solar energy reaching the experimental animal directly through the heating of the atmosphere by the rays of the sun or indirectly through a general insolation of the building in which the experimental room was located. Factor I had a very high loading (.98) on temperature and might therefore be thought to represent the temperature factor. From a philosophical point of view this would be an incorrect identification. Those animals responding to this factor react to a change in the thermal energy level of their immediate environment. A temperature reading is merely another response, measured by a non-living system, to this same energy level and, under the circumstances of our experiment, is apparently the most sensitive indication of the environmental thermal energy level. Light and relative humidity, which we had hoped would be the other two determining factors of our study, appear from the analysis to have no independent effect on the response variables. Their correlations with the response variables can be entirely explained by the effects of the solar energy factor on light and humidity.

The loadings of factor I on these two variables are not very high. Under circumstances other than those of our experiment light and temperature might be more closely correlated, since they are measures of the same source of energy. Under the natural conditions of weather affecting the environment in our room a passing cloud may have drastically lowered light intensity, but the warm air and exposed surfaces maintain their temperatures relatively

constant over a period of time. Furthermore, since the organisms were never exposed to incident sunlight the correlation between temperature and light or between the energy level and the amount of light prevalent in the room was not as high as it might have been.

Similar considerations guide us in explaining the low loading of factor I on relative humidity. In addition it should be pointed out that changes in the absolute water content of the air would of course affect the relative humidity and further reduce the correlation of the energy level with relative humidity. The latter variable was also affected by the time series factor (VI) to be discussed below, which indicated a progressive decrease in absolute water content of the air over the period of the study.

There was an appreciable loading from factor I on the hour of the day. This can be explained, since in general the later the hour of the day the higher the temperature in the room, except for readings performed in the very late afternoon, which were not too numerous. Had such readings not been performed at all the relation between hour of the day and general energy level would have been considerably higher.

Two groups of biological variables were affected by factor I. These were the rates of pulsation of heart and gut and the rates of locomotion. Among the first there were strong effects on roach heartbeat and louse gutbeat while the second group included relatively low effects on wasp and louse locomotion rate. These effects seem eminently reasonable in view of the vast body of literature dealing with the effects of temperature on poikilothermic animals. The interesting aspects of this situation are the four variables in the study falling into these two classes which were not affected by factor I. Two possible explanations are that strong responses to other environmental stimuli, including those introduced by the experimenter in handling and measurement, reduced the effect of the energy factor or that the variables were not linearly related to the energy factor. The former assumption is appropriate in our situation since scattergrams of the variables concerned did not indicate curvilinear relations with temperature. This group of variables includes the heartbeat of flour moth larvae which was moderately affected by factor II, but only to a slight extent by factor I. Since the highest correlation among factors was between I and II (— .30) and since the effect of I on moth heartbeat was of the magnitude of .24, it might be argued that there is at least a part of factor I which determines this variable. However, these relations are of such a low

order of magnitude that we feel hesitant about ascribing any significance to them. The beetle and the housefly rate of locomotion did not appear to have any significant covariation with other variables in the study. The moth rate, on the other hand, had an independent factor unrelated to the energy level determining its variation. These are surprising and disconcerting results. It occurred to us that the wasp and the louse were animals exposed in the experiment to suboptimal conditions compared to those under which they had been reared for many generations. They also had been used to constant temperatures. Contrariwise the beetles and the moths had been accustomed to temperatures fluctuating more or less over the range to which they were exposed during the experiment. We thought that these latter species might therefore be more homeostatic with reference to temperature changes, while the former ones would respond more readily to temperature fluctuations. A difficulty of this interpretation is to explain the absence of response in the housefly larva which was habituated to a reasonably constant temperature of 30° C. One might suppose that the housefly larva should have been the most irritated animal in the study, being accustomed to very high humidities and the protection of medium around it, conditions quite different from those of the experimental glass plate. One may therefore speculate that the rate of locomotion in the housefly larva was a function of its general irritation which overrode the effect of variable temperature.

Factor VI affects four of the physical variables, but none of the biological variables. It is thus an independent dimension of the physical environment. While it is therefore of little interest in interpreting the correlations among our response variables, it does demonstrate the efficacy of factor analysis in isolating the causes of correlation. The factor appears to be a time series factor or trend and can be identified as the passage of time. It informs us that as the days progressed the barometric pressure became higher during the 22 days span of the experiment. Factor VI also has effects on relative humidity and light intensity. The weather became dryer and brighter during the later days of the study. This trend is related to climatic changes which occurred during the period in the Lawrence, Kansas, area. An examination of weather records revealed that there were more cloudy days and more precipitation in the earlier part of the period than in the latter part.

We now turn to a discussion of the biological or behavioral factors revealed in the study. Factor II appears to be a factor primarily

affecting the moth larva. The greater this factor, the more directly away from light a given moth larva will travel and also the straighter its path will be. On the other hand an increase in this factor will reduce the rate of heartbeat of an immobilized larva. It should be kept in mind that the heartbeat was measured on an individual different from the one on which excursion index and angle to light were observed. We do not know the rate of heartbeat in the animal orienting on the glass plate. It is quite probable that immobilization affected the rate that we measured, perhaps by the induction of a pseudocataleptic state while the heartbeat of the moving animal might have increased. The factor analysis, however, shows covariance between the two individuals. The interpretation of factor II is complicated by a negative loading on the angle to light of the flour beetle. This loading, while not of very great magnitude, seems to be the exact opposite of the response of the flour moth larva, *i. e.*, they respond to light in different directions. This is, however, only a relative difference. Both flour moths as well as flour beetles were negatively phototactic under the conditions of the experiment. Factor II determines only their relative aversion to light, which became greater with an increase in factor II for the flour moth and less with an increase of factor II for the flour beetle.

Since factor II (and factor V discussed below) affect the animals' reaction to light, the reader may wonder why under such circumstances the light intensity itself did not have an independent effect on the organism. It is possible that a correlation of response to light intensity is not detected because of a non-linear relationship such as would be produced by a threshold of response in the lower light values. Our scattergrams showed no such curvilinear trends. Therefore, we interpret this phenomenon along the following lines: the organism is stimulated not primarily by the light but by another environmental or behavioral dimension. Its response to the stimulus of factor II is a movement which orients itself by the light. The light is therefore not the critical eliciting factor but is a variable which serves to guide the response of the organism.

Factor III appears to be a factor having to do with the locomotion of the flour moth larva. It is clearly independent of factor II, which also affects the flour moth larva. The number of undulations are primarily responsible for the rate of locomotion, as shown by the high loading on the former variable. The rate of locomotion is, however, not totally determined by the undulations because the flour moths used in the study varied to some degree around the

desired length of 1 cm. There is the disturbing occurrence in this factor of the housefly angle to light. We have stated previously that we believe this to be a spurious correlation.

Factor IV can be interpreted primarily as a wasp factor. The straighter the wasp moves, the faster it will move. This factor also does not seem to correspond to any physical factor measured by us. As previously mentioned wasp rate is also affected by the solar energy factor (I).

Factor V can be interpreted in a manner similar to factor II. It appears to be a factor affecting the louse. As the stimulus increases the louse will move faster, straighter and more directly away from light. Louse rate is also affected by energy level (factor I). Another flour beetle measurement tends to confuse the interpretation of this factor. Factor V will make the beetle go straighter regardless of direction.

We should point out that rate of locomotion and the excursion index are logically entirely independent dimensions of an insect's behavior. Thus a certain species of insect could move either slow or fast and either directly or circuitously, in any of the four possible combinations. On the other hand it might well be that certain insects when moving fast tend to move straighter or tend to move in a more diffuse manner. From the evidence of our analysis it would appear that the wasp and the louse, as seen in factors IV and V, respectively, tend to correlate rate with excursion index, *i. e.*, the faster they move the straighter they move. On the other hand the flour moth appears to have entirely independent dimensions for these two characteristics. In this species there is a positive correlation between directness and angle of locomotion, but not between directness and rate of travel. We might add that the house fly larva and flour beetle behaved similar to the flour moth larva in that their rate and excursion index were independent properties.

d. Discussion and Conclusions

The specific problem of the experiment has been discussed sufficiently and does not warrant further treatment here. However, a few words are in order to evaluate the results in terms of the original aim of the study, namely the demonstration of the value of factor analysis as a tool in experimental biological research.

Of the six factors uncovered in our analysis only one turned out to be a physical factor apparently behind some correlations among the nineteen biological response variables. This factor evidently

represents fluctuations in the solar energy level during the experiment. In terms of the conventional physical variables referred to in such studies it might be labeled "temperature." While a second physical factor emerged it had no effect on the biological variables and the other four factors appeared to be largely species specific or situation specific. These results are due mostly to a poor choice of experimental biological variables, as well as an inadequate measurement of particular features of the environment introduced by the experimenters. Had we chosen appropriate biological response variables it is our conviction, based on the clearly defined structure of present analysis, that the several independent physical dimensions would have shown up quite definitely as factors affecting the correlations. The analysis of our data had the advantage of revealing and evaluating unidentified sources of common variation which would otherwise not have been suspected. Since these sources of stimuli may well be produced by the experimenter's technique or the experimental environment, factor analysis can indicate the need for further control. We are therefore firmly convinced of the value of factor analysis in discovering causal structure in correlated variables and in describing the effects of common factors on response variables.

In view of our present experience we might ask ourselves how an experiment, such as was done by us, might be improved in order that clearer and more interpretable results might be obtained. From the point of view of demonstrating the efficacy of factor analysis it would be far preferable to use one, or at least fewer, species so that species specific factors would be reduced in number if not entirely removed. Some doubt remains in our mind on this point since a study conducted on only one species (but many characters thereof) would very likely exhibit organ specific or organ-system specific factors which again might complicate the interpretation of effects of the physical variables on the biological variables studied. On the other hand, while such a complication muddles the interpretation of the covariation in the study, it is only a reflection of the complicated relationships which are actually found in nature and which belie the arbitrary simplification of biological systems.

The application of better measuring and recording equipment, preferably continuously recording equipment, would be likely to lead to much better and *higher* correlations among the response variables observed. The use of such instruments as minute ther-

mocouples and kymographs applied to the insect in a physiological investigation would surely result in higher correlations, consequently higher factor loadings and presumably in a clearer simple structure.

When adapting factor analytic techniques to a field situation the nature of the problem would have to be taken into account before a correct setup is devised. If we are dealing with a study largely concerned with the physiological effects of the environmental variables on the activity of the insects, then a relatively short term but intensive investigation is called for. Activity variables, such as numbers of insects active, types of activity and rates of activity should be studied in a limited environmental situation together with a considerable number of environmental variables measured simultaneously in that situation. If we are studying factors affecting population growth then the study will have to extend over a considerably longer period of time. It would have to involve climatic records of various sorts, population counts and perhaps such variables as age distributions. It is very likely that in situations such as diapause and predator-prey relationships we would have to compute lagged correlations in order to obtain a high and meaningful correlation matrix.

Persons familiar with factor analysis will be interested in our evaluation of the suitability of a simple structure constellation for biological investigations. We are not prepared at this stage to claim superiority of simple structure over other constellations and feel that a much larger body of data will have to be accrued from a variety of biological fields before even tentative conclusions can be drawn. On the basis of *a priori* consideration each of the customary types of factor constellations, such as principal axes, bipolar factors and simple structure can be defended and situations visualized where these constellations would represent the "true" relationship among variables in nature. It might be added that in the experience of the senior author simple structure has given satisfactory and interpretable solutions in each of the several biological cases in which he has applied it. This problem is discussed in greater detail in the technical companion paper (Sokal, Daly & Rohlf, 1961).

At least two reservations to the use of factor analysis should be added at this point. The problem of the significance of the number of factors extracted, as well as the levels of significance for factor loadings is one that is still quite controversial in factor analysis circles. Whenever a factor matrix is interpreted a real difficulty

develops concerning the level at which a factor loading should be considered significant and an interpretation of it should be attempted. Also there are usually shadowy minor factors which may or may not be significant. Much thought may sometimes be spent on interpreting factors of this nature while considerable doubt will remain regarding their significance. It should also be kept in mind that the relations between factors and variables in the factor matrix are strictly linear. Where the relation among variables and between factors and variables is other than linear one should not expect very meaningful factor resolution. Such variables will have to be transformed into a scale which will be linearly related in order to get meaningful factor structure.

Postscript: During proofreading it was brought to our attention that *Habrobracon juglandis* (Ashmead) as well as *Ephestia kühniella* (Zeller) have both been renamed *Bracon hebetor* Say and *Anagasta kühniella* (Zeller). We have not changed names in this paper since, it would first of all have required much re-editing of the manuscript and since we have doubts on principle about the renaming of organisms well known to the general biological literature.

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Factor Analytical Procedures in a Biological Model [1, 2]

BY

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ABSTRACT: This study attempts to demonstrate the value of factor analysis in a dynamic as contrasted with a static biological model. It also wishes to investigate the efficacy of a simple structure solution, the maintenance of factorial stability in separate and joint matrices and the inclusion of causal variables in the original matrix. Nineteen biological variables were taken from six species of insects. Six physical variables were measured concurrently with the biological variables. Fifty-five replicate readings were taken. Correlation coefficients were computed among the 25 biological and physical variables. Simple structure solutions by the mass modification of Thurstone's analytical method (MTAM) are given for the 19 x 19 response variable matrix, the 6 x 6 causal variable matrix and the 25 x 25 joint correlation matrix. Adequate simple structures are produced by MTAM. Since the reference vectors were largely orthogonal, the varimax solution (Kaiser) and elementary linkage analysis (McQuitty) of the 25 x 25 variable matrix gave essentially identical solutions. Biological implications of the factor analysis are summarized, but details are discussed in a companion paper (Sokal and Daly, 1961). The article concludes with an account of some recent experiences with MTAM, a discussion of the applicability of simple structure to biological matrices, some mention of the stability of the factor solution in separate and joint matrices and our conclusion that including causal variables in the original matrix is a useful technique for identifying causal factors.

INTRODUCTION

Aims of the Study

The present paper discusses certain statistical problems pertinent to the application of factor analysis to a biological model. It originated in an attempt to set up a model with which to validate factor analysis as a tool for discerning cause and effect relationships. Simi-

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lar models have been attempted in the past; *e. g.*, the classical analysis of the dimensions of boxes by Thurstone (1947) or the analagous study of the dimensions of bottles by Barlow and Burt (1954). A study by Dickman of the factors determining the amount of bouncing in balls of different sizes and materials has not as yet been published. The two published studies suffer from the same drawback in that they describe essentially static, geometric situations. Some psychometric theories consider the mind in a static, multidimensional manner. Whereas the authors in their ignorance of psychological theory are not prepared to contest this view, it is our considered opinion that static, geometric models would not reproduce reality in terms of biological processes and therefore would be of little interest for experimental biologists. Since it is also our view that in the biological sciences it should be considerably easier than in psychology to reify factors, it became important to us to construct a model in which known and dynamic factors would be operating. The aim therefore, was to find a series of response variables which would be in part determined by a few, preferably three, causal variables which were well known to the experimenter and which exhibited, in general, relations compatible with the concept of simple structure, *i. e.*, that every factor does not affect every response variable and that any one response variable is not affected by all three factors.

The study was undertaken on insect material, this being easiest obtainable to the authors and the material with which they are most familiar. It was hoped that a study of the response variables (over a series of observations sufficiently numerous to inspire confidence in the resulting coefficients) would yield a correlation matrix which, when subjected to factor analysis, would yield in turn the variables known to be causing covariation in the study. We anticipated that such a demonstration would lend support to the practice of factor analysis and would serve as a stimulus to experimental biologists to consider factor analysis as a complementary or supplementary technique in the analysis of physiological and ethological phenomena. It was expected that a number of points of interest to factor analysts would emerge as byproducts of the study, as follows: (1) The further application of an analytical method for finding simple structure, recently developed by the senior author (Sokal, 1958); (2) The applicability of the concept of simple structure to the case under consideration; (3) The maintenance of factorial stability when correlation matrices are analyzed separately and

subsequently joined together; (4) The inclusion of causal or independent variables in the original correlation matrix. This latter idea has been proposed by Cattell (1952), but has not, so far as is known to the authors, received wide attention or application. The experimental setup and the biological findings are detailed in a companion paper (Sokal and Daly, 1961). Their mention and discussion in the present paper is incidental to its major purpose, namely, a review and discussion of the statistical aspects of the problem and specifically the four points mentioned above.

Limitations of the Study

After considerable experimental effort with a number of insect species, it was found that the desired experimental design was impossible of achievement. A series of variables whose causation was known and in part determined by three major causal variables could not be found. We had to settle for variables whose causation was only partly known, if at all, and whose mutual intercorrelations were not predictable. Furthermore, it was not known whether the relation between causal and response variables would follow a simple structure constellation. When the data were analyzed and interpreted it was found that four of the "causal" variables appeared to share variance with the response variables. Many of the response variables appear to be correlated and determined by causal variables whose nature was unknown and which differed from the ones ini'ially considered.

In the sense of having developed a known dynamic model and then re-established it by means of factor analysis our experiment was thus only partially successful. We feel justified in bringing our findings to the attention of the public interested in factor analysis because of the information we obtained on points 1 through 4 above. As will be seen, our results suggest that wi'h better equipment and more effort a similar model could be designed and reproduced by factor analysis.

MATERIALS AND METHODS

Experimental Materials and Procedures

Table 1 lists the kind of insect and the stage studied as well as the biological variables measured and their code numbers (1-19). The nonbiological variables were the following: (20) temperature in °F; (21) percent relative humidity; (22) atmospheric pressure in inches of mercury; (23) light in foot-candles; (24) the day of the test; and (25) the hour of the day.

TABLE 1.—List of Insect Species Used and Characters Measured

SCIENTIFIC AND COMMON NAME; STAGE OF INSECT	CODE NUMBER AND VARIABLE
Periplanta americana L. American roach, adult.	1. Heartbeat rate
Pediculus humanus DeGeer Human louse, adult or large nymph.	2. Gutbeat rate 8. Rate of locomotion 9. Angle to light 17. Excursion index
Tribolium confusum Duval Confused flour beetle, adult.	4. Rate of locomotion 5. Angle to light 15. Excursion index
Ephestia kühniella Zeller Mediterranean flour moth, larva, 1 cm. in length.	3. Heartbeat rate 10. Rate of locomotion 11. Angle to light 12. Undulation rate 18. Excursion index
Habrobracon juglandis (Ashmead) Parasitic wasp, adult, no more than 5 days since ecdysis. Females only.	6. Rate of locomotion 7. Angle to light 16. Excursion index
Musca domestica L. House fly, 5-day-old larva.	13. Rate of locomotion 14. Angle to light 19. Excursion index

The experiments were conducted in a room illuminated by natural light from a window. The insects were brought to the room and prepared for the test as follows: One of each species, except the roach, was put into a separate vial and a roach, a louse, and a moth larva were immobilized on pieces of glass. Then they were placed for at least an hour in a special container which admitted a current of air from a fan, but excluded all light. After this period of acclimatization, the insects were tested on a horizontal stage of frosted glass opposite the window. Before each insect's performance the temperature, relative humidity and light were measured. Averages of the readings for the temperature and for relative humidity were used as indicative of these variables. Separate light readings were employed since these varied widely during the hour of testing. The pulsations of the dorsal vessel (heart) of the roach and the

moth larva, and the peristaltic waves of the gut of the louse were observed with a binocular microscope in the immobilized insects. They were recorded as beats per minute. The insects in the vials were now released on the stage in a standard sequence and the route of escape of all but the house fly larva was traced in ink on a pane of glass suspended one half inch over the frosted pane. The house fly larva traced its route on the frosted glass with an aqueous solution of methylene blue. Equal units of time were signaled by an assistant and marked along the insects' tracks. Ten of the tracks were less than 5 cm. and were discarded; the remaining routes were traced on paper. Distance between time marks, as measured by a planimeter, gave the rate in cm. per minute. Units of 5 cm. were then marked along the track. The excursion index (linear distance from point of origin to last 5 cm. mark divided by the total distance of the insect's journey to that mark) gave an indication of the extent to which the track deviated from linearity. The 5 cm. marks were now connected by straight lines along the track and the angle measured between each straight segment and a line perpendicular to the window. An average of these angles gave an average angle to light for the track. For insects attracted to light the acute angle was recorded, while for those moving away, the obtuse angle was recorded. An additional variable, the number of locomotory undulations, was recorded for the moth larva. No individual insect was used more than once and there were 55 replications over 22 days. Further details on materials and methods may be obtained from the companion paper (Sokal and Daly, 1961).

Statistical Treatment of the Data

Two minor statistical problems had to be overcome before and during the computation of the Pearsonian product-moment correlation coefficient. The variables had to be transformed in order to approximate normal or at least symmetric distributions. A good many of the variables were extremely skewed and/or bimodal in the scale in which they were recorded. A number of different transformations were tried on each variable where transformation seemed advisable. While we were guided by empirical results of the transformations, logical transformation scales such as reciprocals for rates and square roots for counts were preferred. The following variables required square root transformation: 2, 4, and 23. The excursion indices (variables 15 through 19), which were initially recorded as a proportion and strongly skewed to the left,

improved considerably when transformed into the probit scale. Variables 10 and 12 (both rate phenomena) appeared to be best transformed by taking the square root of the reciprocal of these variables. A positive loading on variables 10 and 12 really corresponds to a deceleration of the rate, while a negative loading achieves exactly the opposite. Variable 14 was transformed by taking the reciprocal of its square.

Variables 24 and 25, days and hours respectively, were not transformed in spite of their non-normal distributions since normal distribution of these variables was hardly to be expected.

The computation of the correlation coefficient was also complicated by the absence of observations for certain variables at given times. This necessitated a particular program to be written for the IBM 650 digital computer which computed correlation coefficients of a correlation matrix with missing observations. The details of this method do not concern us here except to state that the correlations were, of course, based only upon observation pairs and the lower number of observations for any pair of variables determined the number of pairs on which the correlation was based. The minimum number of observations in any one variable was 34 (in variable 17). Only very few variables had that few replications; most variables had around 45, while the maximum number of readings was 55. In computing the significance of correlation coefficients in the resulting matrix the different sample sizes were taken into consideration.

RESULTS

The Correlation Matrix

In order to save space the correlation matrix among the 25 variables is not shown here. For those who are interested it is figured in the companion paper already referred to (Sokal and Daly, 1961). The generally low correlations among the variables observed were a disappointing feature of the study. The average absolute correlation was 0.15. There were 44 significant correlations out of the 300 correlation coefficients in the matrix. This is, however, considerably above the 5 percent level of significance. Our assumption that significant correlation existed in the matrix was borne out by a study of the frequency distribution of the correlation coefficients which turned out to be mildly leptokurtic ($g_2 = .544$, $.1 > P > .05$). Variables 7 and 19 had no significant correlations with any other variable, but were included in the study because it was felt that it would be of interest to observe their behavior during rotation to simple structure.

All computations in correlation work, as well as all subsequent computations, were carried out to 8-place accuracy and were performed on the University's IBM 650 digital computer.

Simple Structure in the 19 x 19 Response Variable Matrix

In line with the aims of the study, the first analysis was carried out solely on the 19 x 19 submatrix of response variables. The matrix was subjected to principal axis factor analysis with reduced communalities. The analysis was repeated three times until initial communality estimates agreed with the computed communalities below a difference criterion of .05. At this point communality estimates were considered stable. The problem of the number of factors to be extracted was attacked by the method of testing for significance of partial residuals as described by Sokal (1959). By this method 5 factors were indicated. The fifth residual matrix showed only three significant partial correlations out of a possible total of 171. This is considerably below the accepted 5 percent level of significance. The findings were borne out by a study of the latent roots of the correlation matrix. An impressive decrease in magnitude appeared between the fifth and sixth latent roots. Subsequent to the original decision a computer program called RESITEST-I was developed by one of the authors (F. J. R.) which enabled us to test the significance of the residuals very rapidly by a variety of methods. The results of these tests for all three correlation matrices are shown in Table 2.

TABLE 2.—Summary of the Decisions on Number of Factors in the Three Correlation Matrices Reached by the Various Methods

TEST EMPLOYED	Matrices		
	6 x 6	19 x 19	25 x 25
Tucker's criterion	2	3? 5? 8	3? 7?
McNemar's criterion	2	5	6
Saunders' criterion	>4	>9	>7
Individual residuals	2	5	6
Humphrey's rule	2	1	3
Number of factors decided upon	2	5	6

The F_0 matrix was rotated to simple structure using the mass modification of Thurstone's analytical method (MTAM) as developed by Sokal (1958). The simple structure obtained by the MTAM method was reiterated three successive times. The aim in this undertaking was to see whether increasingly improved simple structure could be obtained on successive reiteration by the MTAM method. Surprisingly it turned out that fewer variables were in the hyperplanes at the later than at the earlier iterations. Also, various test vectors began to become correlated during the later iterations. These findings seem to contradict the senior author's earlier supposition (Sokal, 1958) that on successive iterations the simple structure would be improved. We therefore used the first of the itera-

TABLE 3.—MTAM Simple Structure and C_R Matrices of 19 x 19 Correlation Matrix

	Variable number	Reference vectors				
		I	II	III	IV	V
Roach beat	1.	71	16	−16	04	−02
Louse beat	2.	64	47	13	24	00
Ephestia beat	3.	42	−38	03	21	−33
Tribolium rate	4.	04	−21	−31	10	−17
Tribolium angle	5.	04	−39	00	05	36
Habrobracon rate	6.	39	10	−31	−22	−10
Habrobracon angle	7.	−03	−10	07	−21	−06
Louse rate	8.	48	02	09	−12	41
Louse angle	9.	−11	−03	−06	06	63
Ephestia 1/rate	10.	08	06	56	−04	−21
Ephestia angle	11.	20	67	−00	09	00
Ephestia 1/undulations	12.	−11	−03	89	−11	06
Musca rate	13.	10	08	−22	47	−02
Musca 1/angle	14.	−08	06	44	−34	−27
Tribolium index	15.	−01	−01	−05	08	45
Habrobracon index	16.	10	−12	−28	−70	−15
Louse index	17.	05	03	20	−09	73
Ephestia index	18.	03	44	−40	04	02
Musca index	19.	−28	15	−09	08	−07
		C_R				
		I	II	III	IV	V
	I	X	30	−10	04	05
	II	30	X	07	02	−07
	III	−10	07	X	−19	−21
	IV	04	02	−19	X	−02
	V	05	−07	−21	−02	X

Decimal points are omitted before coefficients in this and following tables.

tions, which gave by far the best simple structure. The simple structure matrix is reproduced in Table 3, which also shows the correlation between the reference vectors (C_R matrix). The table shows that three variables (4, 7, and 19) had no loading larger than 35. This was to be expected since these three variables had very low communalities. A discussion of the significance of this matrix will be postponed until a later section.

Simple Structure in the 6 x 6 "Causal" Variable Matrix

The 6 x 6 correlation matrix of the so-called causal variables was subjected to a principal axis factor analysis with reduced communalities in the diagonal. The procedure followed was very similar to that described in the previous section for the 19 x 19 response variable matrix. It took three iterations to stabilize the communalities within the criterion of .05. A number of tests of completeness of factor extraction were performed which in summary indicated that two common factors sufficed to account for the covariance in the matrix (see Table 2). The first cycle of the MTAM procedure resulted in a very satisfactory simple structure

TABLE 4.—MTAM Simple Structure and C_R Matrices of 6 x 6 Correlation Matrix

	Variable number	Reference vectors	
		I	II
Temperature	20.	–04	96
Relative humidity	21.	–49	–71
Atmospheric pressure	22.	73	01
Light	23.	27	59
Day of month	24.	77	02
Hour of day	25.	–26	54
		C_R	
		I	II
	I	X	–07
	II	–07	X

for the two factors and it was not deemed necessary to reiterate. The simple structure matrix is shown in Table 4. The correlation between the two reference vectors is .07.

Simple Structure in the Joint 25 x 25 Variable Matrix

For the factor extraction of this matrix we could not employ the principal axis program used to extract the previous two matrices. With the program available to us several hours of computation time would have been necessary per iteration even on the digital computer. The method adopted therefore was Thurstone's complete centroid extraction (using a computer program developed by one of the authors [F. J. R.]), which was carried out with reduced communalities and repeated through six complete iterative cycles. This was more than the necessary number since at the end of the sixth iteration the communalities were stable within a tolerance of .002. While it is not entirely desirable that a changeover be made in the method of extracting factors, it was on the other hand reassuring to us to find the close relation between the submatrices which were factored by the principal axis method and the 25 x 25 matrix which was factored by the centroid method. In estimating the number of factors to be extracted we were guided by several considerations. Saunders' criterion gave more than seven factors, Tucker's criterion was indecisive. The criteria of McNemar and of significant partial residuals both yielded six significant factors. We concluded that six was probably the correct number (see Table 2). The method of significant partial correlations and some of the other criteria ran into difficulty because of the high communalities found. This is a common situation likely to lead to confusion. When seven factors were extracted experimentally and the number of significant partial correlations remaining was computed, it was found that a higher percentage of such correlations was present than in the sixth residuals. This indicated to us that most remaining significant residuals were artifacts produced by the high communalities and consequent low uniquenesses.

The MTAM analysis was performed through only one iterative cycle and the results therefrom are given in Table 5. The simple structure which emerged is quite satisfactory when the various criteria for simple structure are considered. There are, however, four variables (4, 7, 13 and 19) which do not appear to have important loadings ($\geq .35$). The correlations among reference vectors shown in the same table indicate generally orthogonal relations with

TABLE 5.—MTAM Simple Structure and C_R Matrices of 25 x 25 Correlation Matrix

	Variable number	Reference vectors					
		I	II	III	IV	V	VI
Roach H.B.	1.	72	05	−05	14	04	−03
Louse Gut B.	2.	61	33	21	−20	09	−17
Ephestia H.B.	3.	23	−57	05	−07	−34	−01
Tribolium rate	4.	08	−23	−32	06	−25	−12
Tribolium angle	5.	−10	−44	−02	−04	33	−05
Habrobracon rate	6.	38	07	−24	48	−04	−11
Habrobracon angle	7.	−12	−11	06	32	−01	22
Louse rate	8.	40	−04	11	11	44	07
Louse angle	9.	−06	10	−05	−03	56	04
Ephestia 1/rate	10.	14	−01	58	−09	−17	08
Ephestia angle	11.	27	62	03	01	13	01
Ephestia 1/undulation	12.	00	−02	91	−28	05	−02
Musca rate	13.	21	07	−14	−31	−13	09
Musca 1/angle	14.	−05	12	48	13	−23	−12
Tribolium index	15.	−20	−08	−10	−04	49	02
Habrobracon index	16.	07	03	−32	90	−06	−15
Louse index	17.	09	10	17	−09	77	−01
Ephestia index	18.	06	40	−33	09	05	03
Musca index	19.	−20	24	−06	−05	−14	15
Temperature	20.	92	20	01	07	−04	07
R.H.	21.	−60	01	02	08	08	−53
Pressure	22.	10	17	−24	−01	21	63
Light	23.	53	−16	01	05	−23	41
Day of month	24.	03	−01	08	−13	02	83
Hour of day	25.	48	−07	−17	−06	−15	−27
		C_R					
		I	II	III	IV	V	VI
	I	X	32	11	09	05	03
	II	32	X	14	08	13	−12
	III	11	14	X	−22	−15	−01
	IV	09	08	−22	X	14	−01
	V	05	13	−15	14	X	−01
	VI	03	−12	−01	−01	−01	X

the possible exception of reference vectors I and II, correlated to the extent of .32.

A remarkable feature of the analysis became apparent, when it was noted that the factor loadings observed in the 25 x 25 matrix were nothing but composites of the factor loadings observed in the 19 x 19 and 6 x 6 matrix. Factor I of the 19 x 19 matrix and factor II of the 6 x 6 matrix re-emerged as factor I of the 25 x 25 matrix. Fac-

tors II through V of the 25 x 25 matrix were numbered to correspond with factors II through V of the 19 x 19 matrix, which they match. Factor I of the 6 x 6 matrix is factor VI of the 25 x 25 matrix. The relative invariance of the results from the three matrices lends encouragement and support to our belief that the MTAM method does produce a reasonably unequivocal simple structure and that the simple structure solution itself is a relatively meaningful position for the data shown here. The latter belief, however, will need further justification, which we hope to provide in the following sections.

The Varimax Solution and Centroid Linkage Analysis

An alternative method of taking the data to simple structure is the Varimax method developed by Kaiser (1958). Through the courtesy of Dr. Kaiser we were able to process our 25 x 25 matrix on the ILLIAC computer using the Varimax routine. Table 6 shows

TABLE 6.—Varimax Simple Structure of 25 x 25 Correlation Matrix

	Variable number	Reference vectors					
		I A	V B	III C	VI D	II E	IV F
Roach H.B.	1.	76	01	−06	−02	05	04
Louse Gut B.	2.	57	−09	17	10	−20	−30
Ephestia H.B.	3.	34	31	04	00	62	−03
Tribolium rate	4.	16	30	−33	10	20	00
Tribolium angle	5.	−01	−38	−02	06	47	01
Habrobracon rate	6.	43	15	−22	11	−06	38
Habrobracon angle	7.	−11	02	10	−17	08	38
Louse rate	8.	43	−44	12	−08	13	09
Louse angle	9.	−07	−57	−05	−04	−09	−04
Ephestia 1/rate	10.	08	09	58	−06	10	−01
Ephestia angle	11.	15	−07	03	−04	−61	−08
Ephestia 1/undulation	12.	−06	−21	90	05	16	−14
Musca rate	13.	17	15	−17	−16	−07	−36
Musca 1/angle	14.	−09	18	50	17	−07	19
Triboleum index	15.	−18	−51	−10	−01	06	−02
Habrobracon index	16.	15	21	−25	22	−08	84
Louse index	17.	08	−81	17	01	−02	−08
Ephestia index	18.	01	04	−32	−06	−46	−01
Musca index	19.	−27	15	−06	−14	−31	−04
Temperature	20.	92	11	00	−14	−08	−06
R.H.	21.	−56	−09	02	59	−04	10
Pressure	22.	01	−17	−21	−65	−26	00
Light	23.	53	25	03	−45	19	05
Day of month	24.	−08	−05	12	−83	−06	−03
Hour of day	25.	55	19	−20	21	15	−17

Reference vectors are identified by capital letters. The Roman numerals refer to the reference vectors from Table 5 which the Varimax vectors resemble.

the Varimax simple structure solution of the 25 x 25 correlation matrix. Readers will be struck by the similarity of this solution with that shown in Table 5 by the MTAM method. The Varimax solution is an orthogonal solution forcing the reference vectors to remain uncorrelated. It was to be expected that this solution would be similar to the one found by MTAM since in this particular case the reference vectors were not very correlated, the highest correlation coefficient being .32 between reference vectors I and II. It must not be assumed, however, that in cases where the correlation between reference vectors will be high Varimax and MTAM are likely to give the same solution.

We also undertook an elementary linkage analysis (McQuitty, 1957) of the 25 x 25 correlation matrix. This yielded five clusters which contained the same variables as five of the six factors which eventually resulted from the simple structure analysis. A similar result was obtained when centroid linkage analysis (McQuitty, 1957) was applied to the 6 x 6 matrix. When factor loadings were estimated from the centroid linkage analysis, using the known communalities of the 6 x 6 matrix, the typal relevancies agreed to within .04 with the factor loadings obtained by MTAM. It is not surprising that these various methods of cluster and linkage analysis yield results similar to Thurstone's method for simple structure, since as was mentioned previously, the correlations among the reference vectors in this study were relatively low. Whenever the factors are discrete and have very little correlation among themselves, separate non-overlapping clusters are formed in the correlation matrix and are often quite easily discernible by simple methods of cluster analysis. This is not to recommend cluster analysis in place of factor analysis, because in cases where factors would have large areas of overlap or be highly correlated with each other cluster analysis would be of no particular value.

DISCUSSION

Biological Implications

Since a suitable test of significance for factor loadings is lacking, we have arbitrarily selected a level of .4 as the lower limit for important loadings. The six factors can be clearly separated into two kinds: physical and biological. These two categories of factors affect only a few variables in common.

Factor (VI) did not affect biological variables. It loaded highly on "day of experiment," indicating a time series trend over the span

of the experimental period. During this period pressure increased, the atmosphere became drier and average light intensities during the observations rose. The last two variables, as well as "hour of the day," are affected by the second physical factor (I) which is closely related if not identical with temperature. This factor is more properly regarded as a measure of the general solar energy of the environment. This energy factor was the only physical factor with appreciable loadings on biological responses, *i. e.*, rates of pulsations of the roach heart and louse gut. These rates were probably also affected by the immobilization required for observation as well as by physiological condition of the insect. The predominant influence, however, is that of the energy level which is a relationship to be expected in cold-blooded animals.

Two rates on locomotion, that of the wasp and that of the louse, are also affected by Factor I. These two variables load on additional factors. A wasp factor (IV) shows loadings on the above rate as well as high loadings on wasp excursion. This means that wasps tend to run much straighter with an increase in rate of travel. The remaining wasp variables, angle to light, shows no covariance with the other variables in the study.

In a similar manner, the louse rate is affected not only by the energy factor, but also by a factor (V) which influences all the remaining louse characters. An increase in this special factor means an increased rate of locomotion and a much straighter route directed more away from light. Factor V also has loadings on the excursion index of the beetle. This would indicate a common source of stimulation not measured as a physical factor. Such a source may have been provided by the experimenter in handling and measurement of the insects, by irregular vibrations in the building, or by visual patterns in the room which influenced certain features of the escape routes of the two species.

The beetle's angle to light is affected by a factor (II) which otherwise shows loadings only on characters of the flour moth larva. This is the second factor in which the source of stimulation is unknown. The rate of locomotion of the beetle showed no covariance with other variables in the study. An increase in factor II gives a route more toward the light for the beetle while for the moth larva, it gives a straighter route more away from the light. The different orientations to light are only relative since both species were repelled by light. The heartbeat of the immobilized flour moth larva is reduced by an increase in this factor. It should be remembered

that the heartbeat and the features of the route were measured on different individuals of the larval form. While the analysis shows covariance between these characters we suspect that the heartbeat of the larva was affected by the confinement and probably different from the unmeasured heartbeat of the larva orienting on the glass plate.

Finally, the rate of locomotion and the number of undulations of the flour moth larva are affected by Factor III. In this case it is obvious that the undulations are the primary locomotory movements, but this relation is not absolute. The loading of the house fly larva apears to arise from a spurious correlation.

The relationships shown by the analysis are reasonable in most cases. The complications are found in those factors which lack loadings on physical variables, but influence more than one species of insect. The mixture of species affected by Factor III is probably the result of spurious correlation. The mixtures in Factors II and V seem to indicate common stimuli whose sources are unknown. It is quite possible that the source is provided by the experimenter's activities, treatment of the insects, and the experimental apparatus. If this is the case, the analysis has revealed and evaluated appreciable components of variation which would have been routinely lumped as experimental error. It is not unusual that the experimenter represents a dynamic influence in the experimental environment. A more detailed discussion of the factors can be found in Sokal and Daly (1961).

Factor Analytic Implications

(*a*) Further experiences with the mass modification of Thurstone's analytical method

The method for arriving at simple structure employed in this paper was developed by the senior author (Sokal, 1958). The reference just cited included the application of the method to four matrices from various biological sciences which yielded satisfactory simple structures by the method abbreviated as MTAM. Since the above work was done, two of the present authors (R. R. S. and F. J. R.) have had considerable experience in applying MTAM to other correlation matrices. In addition to the three matrices discussed in the present paper a Q-type matrix involving correlations among 23 species (the matrix used as an example in Sokal and Michener, 1958) was rotated to simple structure, as well as five smaller matrices of dimensions from 9 to 14 based on a variety of biological

situations. All of these yielded simple structures which by the criteria stated appear to be satisfactory.

In carrying out the steps for an MTAM analysis we became concerned whether the empirical procedure suggested by the senior author (Sokal, 1958, pp. 251) would bias the simple structure along either of the two criteria used to establish it. Test vectors are chosen both by the number of variables which each reference vector carries in its hyperplane as well as by the number of low correlations with other reference vectors. Exclusive emphasis on the former criterion would yield simple structures with a maximum number of variables in the hyperplanes, in extreme cases with almost specific factors, while these factors could potentially be quite highly correlated. On the other hand overemphasis on the second criterion could result in an essentially orthogonal factor matrix but with not clearly defined factors which might have intermediate size loadings on many variables.

It has been our experience with these various matrices that we were rarely, if ever, put before the difficult choice of evaluating one criterion against the other. If a variable was satisfactory by one criterion it was in general satisfactory by the other criterion. In cases where the two criteria did not match up it has been our consistent policy to give somewhat greater weight to the criterion of number of variables in the hyperplane, rather than that of low correlations, since we feel that such requirements are more in the spirit of the simple structure. The inclusion of a criterion preferring orthogonal factors (all other things being equal) resulted in quite low C_R matrices in our study, as can be seen in Tables 3, 4, and 5. It should be pointed out that MTAM does not require orthogonality of reference vectors *per se*. It chooses reference vectors which are orthogonal to many other reference vectors but which are not necessarily orthogonal to specific vectors chosen for our analysis. While the reader may get the impression that orthogonality is a principal goal when he examines the C_R matrices in this paper, C_R matrices in other studies showed appreciable high correlation coefficients.

It has been our general experience that the number of clusters of reference vectors which are established as part of the MTAM procedure is usually close if not identical to the number of factors that have been extracted. Thus in the 25 x 25 matrix, where six factors were extracted we found six reasonably clear clusters of reference vectors in the C_R matrix. Similarly in the 19 x 19 matrix, where

five factors were extracted, five clusters emerged and in the 6 x 6 matrix only two clusters appeared, matching two extracted factors. These findings are also borne out by similar studies on other matrices.

By way of an experiment we re-analyzed the 25 x 25 correlation matrix by Thurstone's complete centroid method, but only extracted three factors, knowing this number to be too low. We iterated to stability on three factors and then subjected the resulting factor matrix to an MTAM analysis. Three, possibly four clusters of reference vectors resulted. One of these clusters appeared to represent factor I as established by the previous analysis; the others could not readily be identified with any of the previous factors and did not appear to provide more interpretable solutions.

Underextraction thus appears to lead to unclear results. While one or more factors may be identical to those which might result from MTAM analysis of a complete extraction, most factors from the underextracted matrix would probably differ and be less desirable. MTAM, however, does not provide an easy check demonstrating underextraction of the correlation matrix.

It is our expectation, which we have not yet been able to corroborate, that overextraction of the matrix by the centroid method and subsequent MTAM treatment would bring out the fact that too many factors had been taken out. This might come about by finding fewer clusters of reference vectors in the C_R matrix. If as many clusters appeared as extracted factors the supernumerary vectors might have low and confused loadings on the variables.

We have already stated previously that the iteration of the $V_{j\wedge}$ does not provide increasingly clear simple structure although the senior author had earlier supposed that it would (Sokal, 1958). Extensive corroboration of this point will have to await improved computational methods as the re-iteration of a sizeable matrix is still a tedious undertaking.

Since the first publication of the MTAM method the computation has been considerably simplified by having most of the steps programmed for the IBM 650 digital computer with indexing accumulators and floating-decimal arithmetic by one of the authors (F. J. R.). The program is entitled Matrix IV and uses the output of a complete centroid extraction as input. It will perform almost all the necessary computations except for the weighting, which is carried out by another program called MATRIX WEIGHT, and the matrix inversion which requires the program entitled INVERSE

SYMMETRIC MATRIX (by U. W. Hochstrasser modified by Rohlf). MATRIX IV as written now requires the repeated passing of the data through the digital computer. Ideally the data should be subjected to MTAM with one pass through the machine, but this cannot be done on the limited memory (2000 words) available on an IBM 650 without accessory storage units.

(*b*) The applicability of simple structure to biological matrices

The use of the simple structure constellation has been a somewhat controversial one in the psychometric literature. Different schools of thought have developed regarding it both in this country and in England. The authors are not prepared within the context of the present paper to review the history of the controversy nor even to outline the main positions of the protagonists. On the other hand it seems to us that some justification is necessary for rotation to simple structure in a biological matrix.

Simple structure is a hypothesis of simple factors in nature representing the action of few forces in relatively simple patterns. This concept, epitomized by *natura est simplex,* which was in vogue from the beginning of experimental biology in the late 19th century until the first two decades of the present century, has lately gone out of fashion. However simple and elegant a biological concept may be and however necessary it may be to simplify initial biological hypotheses in order to be able to prove their existence, subsequent study and penetration of the problem invariably results in relations considerably more complex than they were initially believed to be. This is true even for genetics, the biological science most often held up as a model of exactness and simplicity. Modern genetics honors the Mendelian laws by their breach rather than by their observance. Initially simple "diagrammatic" phenomena such as sex determination have been shown, in any organism in which they were carefully examined, to be quite complex, depending on equilibrium conditions of a whole series of factors. Whatever branch of biology one chooses, be it physiology, endocrinology, developmental mechanics or evolutionary mechanisms, one finds therein consistently a multiplicity of factors interacting in a most complex manner to produce the results which are observed and studied. Is it therefore plausible that we should simplify complex phenomena of covariation among variables by reducing them to a few dimensions, each of which affects only a very few of the total array of characters?

A second doubt arises from the problem of the number of factors to be extracted from a correlation matrix. Classical factor analytic

theory has tried to relate the number of factors to the rank of the matrix. Attempts have been made to test for the significance of the residuals left after a number of factors have been extracted. In a provocative recent article Cattell (1958) re-examined this entire problem of number of factors to be extracted. He reasons, and very cogently so, that undoubtedly each correlation matrix is caused by many more factors than there are variables in the study. Therefore the question of the number of significant factors which can be extracted from a correlation matrix, which is customarily assumed to be smaller than the dimension of the correlation matrix, is really meaningless. Thus the entire matter of testing for the significance of residuals, which has never been in a very satisfactory state, is reopened.

We bring up Cattell's opinion largely to show that it may be erroneous to suppose that only a few factors determine covariation in a matrix. It may well be that the factors which we extract are purely mathematical constructs, which conveniently summarize the information given by the correlation matrix but do not at all represent reality. Had each of these many factors roughly equal and low influence on all the variables in the study, a vague, perhaps indeterminate and certainly meaningless structure would result during a factor analysis. On the other hand, if factors are unequal in their importance and unequal in their effects on different variables, it may well be that a structure somewhat similar to the simple structure pattern may be found. We may question whether we have a continuum of factor loadings from very high to negligibly low loadings or whether the distribution of the magnitude of these loadings is bimodal or multimodal so that a series of definite, partly overlapping clusters is formed by the effects of the factors on the variables. Simple structure solutions as practiced today usually show bimodality of loading magnitudes. As a matter of fact some of the analytical solutions proposed (see Saunders, 1953; Neuhaus and Wrigley, 1954; Kaiser, 1958) in effect force bimodality upon the loadings. It seems difficult to see any *a priori* reason for bimodality. One would rather suppose that factors had an entirely continuous gradient of effects on variables.

When the cause-and-effect system is looked at from the point of the characters or variables, we are led to ask how many factors affect each variable. Simple structure would indicate that only few of the factors in the study affect any given character. However, it may quite legitimately be claimed that to some degree all of the factors

affect a given character. Genetic mechanisms presumably underly many of the biological phenomena studied. An appreciable number of geneticists would tend to support the idea that every gene affects every character. There must then be an entire spectrum of gene action from the most drastic and immediate kind of effect to the most subtle pleiotropic effect of a gene upon another character.

Philosophical reasons may exist for preferring one or the other of these contrasting views, *i. e.*, for preferring bimodality of loadings vs. a gradient of factor effects. Empirical evidence from a variety of situations is required to resolve this issue. A study of many simple structure matrices is not likely to yield such empirical information because the simple structure constellation deliberately rotates (and possibly distorts) the relationships between factors and variables into bimodality.

The senior author has had serious misgivings about the validity of simple structure since he first became interested in factor analysis. As may be evident from the above discussion he still harbors grave doubts about the method. However, actual results in a series of different researches have demonstrated that simple structure has invariably given a more meaningful interpretation to the data than did either a straight centroid extraction or even a principal component analysis. While the simple structure solution in the present study yielded several factors which were difficult to interpret, inspection of the unrotated centroid and principal axes factor matrices showed these to be considerably less clear than the rotated constellation. Until further insights and work are brought to bear upon this problem it will tend to remain in its present state of uncertainty.

(*c*) The stability of the factor solution

Brief mention should be made of the stability of the factor solution, when the separate 19 x 19 and 6 x 6 matrices were analyzed jointly in the 25 x 25 matrix. It has already been pointed out (and the reader can again confirm it by referring to Tables 3, 4, and 5) that the loadings obtained by a separate analysis of these matrices are very similar. We are thus able to recognize easily in the 25 x 25 matrix the factors which were isolated separately in the 19 x 19 and 6 x 6 matrices. This situation recalls factorial invariances but cannot properly be so called since we are not dealing with an independent selection of variables. We can, however, demonstrate that the shifts in the center of gravity of a matrix resulting from the addition of the new variables has not been such as to result in a different simple structure solution.

(*d*) The inclusion of causal or independent variables in the original matrix

One of the functions of factor analysis in the exploratory stage is to delineate the nexus of cause and effect variables and to attempt to arrange these in order of causation. This may be quite difficult as Cattell (1952) has pointed out, in that many social and biological cause-and-effect relationships are really circular interactions. At the biological level which we are studying and in the particular type of data analyzed in this paper circular interaction is not likely to have taken place, at least not between the physical and the biological variables. The temperature of the room is not likely to have been materially altered by the activities of the insects therein, although it might have been affected by the activities of the investigators. Similarly, light and relative humidity were probably unaffected by the responses of the insects. The other "causal" variables were evidently quite independent of the biological response variables.

Cattell (1952) supposed that among the variables loaded by a given factor the one that is loaded the highest is likely to be the cause or factor itself. While Cattell does not expostulate on this point it seems to us that only in cases where the loading between the factor and a given variable is very high is it likely this variable is the cause of some of the other correlated variables affected by the same factor. In any case the inclusion of possibly causal variables, as in our study, does provide the opportunity of reifying some of the factors.

When we examine our data we find that two of the factors, namely factor I (the solar energy factor) and factor VI (the time series factor) have high loadings on variables which we had thought likely to be common causes in our study. Solar energy has a loading of .98 on temperature which makes the two practically synonymous. However, an interesting philosophical point requires discussion. While temperature is the common measure for solar energy the latter cannot strictly be identified with temperature. Temperature as measured by us and by most investigators refers only to a state of molecular excitation exhibited by a column of mercury in a special device (a thermometer) or pertains to a property of a physical element of some other type of temperature-measuring apparatus, such as change of resistance in a thermocouple. The amount of solar energy received by a given surface would be difficult to measure and would vary with the type of surface and other environmental conditions. However, the biologically significant

temperature concerns only the amount of heat received by a given organism, or better still, by certain specific portions of a given organism performing a specified metabolic task. In studying the effect of temperature on the heartbeat of the roach, for instance, we are concerned with the energy level of those portions of the insect's anatomy which participate in and affect the heartbeat. Thus the temperature of the room is only indirectly causal to the energy level at which the insect performs its function. This rather obvious point has been made in great detail in order to show that certain variables which commonly are thought of as causal might not in the strict sense be so considered. Thus we might have an elusive, somewhat abstract, factor called solar energy which affects a number of these variables such as temperature, roach heartbeat, louse gut-beat and others without any one variable being causal to any other *sensu strictu.* On the other hand, we may wish to use the terms "cause" and "effect" more loosely, partly with a view to an economy of language, and may still use the criterion of the largest loading to identify causal factors. We might then state that temperature is the cause which affects the variables loaded by factor I. In a simpler sense, and probably more justifiably so, days (which refer to the passage of time) are the cause of the time series factor (VI). It is interesting to speculate whether high loading variables on the other four biological or situation specific factors are also causal. In the case of factor III the answer is surely in the affirmative. Moth undulation appears to be nothing but the basic locomotion of the moth, which is not completely correlated with the rate of locomotion because some of the undulation movements are not very productive by way of moving the larva along. In IV and V, where wasp excursion index and louse rate, respectively, are the highest loading variable, the interpretation becomes difficult. It is our firm opinion that had there been more causal variables in the study, these would have shown up in the same variable clusters with the biological variables dependent on them. Thus the inclusion of possible causal variables is to be highly recommended in exploratory studies.

POSTSCRIPT: During proofreading it was brought to our attention that *Habrobracon juglandis* (Ashmead) as well as *Ephestia kühniella* (Zeller) have both been renamed *Bracon hebetor* Say and *Anagasta kühniella* (Zeller). We have not changed names in this paper since, it would first of all have required much re-editing of the manuscript and since we have doubts on principle about the renaming of organisms well known to the general biological literature.

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The Bionomics of a Primitively Social Bee, *Lasioglossum inconspicuum*[1]

BY

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ABSTRACT: *Lasioglossum inconspicuum* is a common small halictid bee in eastern North America. It nests solitarily or in loose aggregations. The nests are in the ground, in sunny areas of bare soil. The burrows are deep, more or less vertical, with subhorizontal cells along them (Figures 5 to 16). This species visits a wide variety of flowers (Table I) but largely ignores the extensive flora of yellow autumnal Compositae. Afternoon activity on flowers is markedly less than that in the morning, and a much smaller percentage of the bees that are afield collect pollen in the afternoon than in the morning. A brief midday drop in activity is indicated by the observations (Figure 1).

Overwintering occurs as fecundated queens in the nests used the previous season; these queens begin spring activities in late March or April. Most of them establish new nests as lone individuals but some remain in the overwintering nests. Sometimes as many as six queens or potential queens may jointly occupy an old nest. There is evidence that in such cases some of them sometimes have a workerlike rather than egg-laying function. The mortality of colonies is very high throughout the season (Figure 4) but the reasons for the high mortality are not clear.

The queen nests, whose cells are provisioned by queens in the spring, become closed in May and are reopened by emerging workers at the end of May or in early June. The nests are then enlarged, a process which goes on (if the colony survives) through the summer. The queen lays more eggs as cells are completed and provisioned during the summer. During this time the queens do not leave the nests with the frequency of workers, but possibly do so less frequently to feed. They do not collect pollen. Their mandibles, however, become progressively more worn, indicating that they work in the nest. Some queens die during the summer and are seemingly replaced by young females. Such replacement queens do not survive the following winter.

Workers, in contrast to queens, are quite short lived, surviving as adults for perhaps three weeks. Some workers have one or even two ovarioles enlarged and presumably lay a few eggs (Figure 28). Such egg-laying workers collect

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pollen freely and seem to act otherwise like typical workers. Young workers act as guards and become lost if removed from the nest. Older workers do the foraging except in spring when the queens are establishing their colonies. The number of foraging trips per unit time varies greatly (Table II), as does the duration of such trips (Figure 3).

Males are absent in the first broods produced by overwintered queens but appear in small numbers in June, much larger numbers in August and early September (Figure 22).

The average number of females in a colony varies seasonally as shown in Figure 21; there is very wide individual variation in colony size as shown in Table VII.

Workers average smaller than queens (Figure 31), but in some nests the largest worker is larger than the queen. Egg-laying workers average larger than those with slender ovaries, but smaller than queens. The mean size of workers in July is smaller than in June or August. A similar seasonal fluctuation in size of males was noted (Figure 23).

There is no evidence of communication among individuals of a colony. The return of a forager does not seem to constitute a stimulus for other foragers to leave the nest. The guards seem quite unable to distinguish individuals of their own colony from those from other colonies. Young workers that have not yet been afield and learned the location of their own nest can be transferred to another nest where they soon function as guards and live out their lives, their alien origin apparently not recognized. Workers that are older, if transferred to another nest, soon leave it and return to their own nest.

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INTRODUCTION

This paper provides an account of the life cycle and behavior of one of the primitively social halictine bees, *Lasioglossum (Chloralictus) inconspicuum* (Smith). This study is part of an investigation of comparative halictine behavior intended to shed light on the origin and evolution of social behavior and castes. Observations were made over a period of eight years in the vicinity of Lawrence, Kansas. During several of those years efforts were made to follow the life cycle as completely as possible; during other years our efforts were directed toward elucidation of certain details of the life cycle or behavior. The methods used are largely those described by Linsley, MacSwain and Smith (1952) and by Michener, Cross, Daly, Rettenmeyer and Wille (1955), although many of them are further explained in appropriate places below.

Over 200 nests were excavated and 929 females were dissected to determine the condition of the ovaries, spermatheca, and crop, examined to determine mandibular wear and measured to determine size. Hundreds of other observations on living marked and unmarked bees were made, so that for example, we have about 125 records of the duration of pollen collecting flights of individual females.

Probably a majority of the species of the enormous subfamily Halictinae are social to a greater or lesser degree. The several bees inhabiting a single nest are said to constitute a *colony;* groups of nests placed close to another another constitute an *aggregation.* Since social behavior evidently arose repeatedly and independently

in various evolutionary lines within the subfamily, this group offers unparalleled opportunities to investigate incipient and primitive societies. A synthesis of the available information on halictine behavior and evolution will be presented later. It will suffice here to give a brief account of previous works on the biology of the subgenus *Chloralictus* [1]. *L. opacum* (Moure) from Brazil appears to be a solitary bee without strong aggregative tendencies and without a worker caste (Michener and Lange, 1958). Presumably males and females appear in roughly equal numbers throughout the season.

In *L. rhytidophorum* (Moure) (see Michener and Lange, 1958) and probably in *L. seabrai* (Moure) and *guaruvae* (Moure) (see Michener and Seabra, 1959), small colonies exist in which there are weakly differentiated queens and workers. At least in *rhytidophorum* the queens, of which there are usually two or more per nest, are rather frequently replaced and males are produced throughout the reproductive season, although in smaller numbers in summer than in spring and fall. In *L. inconspicuum* the colonies are larger, there is more often only one queen in a nest, more workers are produced per queen, workers and queens are a little better differentiated, and queens probably often survive for most of a year. Males are not or scarcely produced early in the reproductive season (spring and early summer), appear only in moderate numbers in midsummer, but become abundant in the autumn.

The nest architecture is known for more species of *Chloralictus*. In addition to those listed above it is known for *L. pruinosum* (Robertson) (see Melander and Brues, 1903), *rohweri* (Ellis) (see Sakagami and Michener, in press), *smilacinae* (Robertson) (see Brittain, 1933), *versatum* (Robertson) (see Sakagami and Michener, in press) *zephyrum* (Smith) (see Sakagami and Michener, in press) and for perhaps half a dozen unidentified species. In all of these the nests are similar, each consisting of a branching main burrow from which diverge subhorizontal, bilaterally symmetrical, wax lined cells connected to the main burrow without or by very short lateral burrows. Only in *L. aricense* (Schrottky) (= *Halictus glabriventris* Friese) and *herbstiellum* (Friese) (see Claude-Joseph, 1926) from Chile are the basic features of the nest architecture different from that of the above species. Possibly these forms are not properly included in *Chloralictus*, or perhaps they were misidentified by Claude-Joseph.

A small amount of information on nests and behavior of *L. in-*

1. Australian species included in *Chloralictus* by Rayment in various publications treating of biology are in reality not related to *Chloralictus*.

conspicuum is found in the papers by Michener, Cross, Daly, Rettenmeyer and Wille (1955), Michener (1958), and Michener and Lange (1958). In these publications the synonymous name, *stultum* Cresson, is used for this species. The meager conclusions on this species presented in those papers appear in greater detail in the present work.

We wish to acknowledge grants from the National Science Foundation which made the study possible. We wish also to thank several persons who helped with the field observations. This has been no light task, as those who have spent long hours on the ground watching or digging bees' nests in the hot summer sun can testify. The persons concerned are Earle A. Cross (now of Northwestern State College, Natchitoches, Louisiana), Howell V. Daly (now of the University of California, Berkeley, California), Wallace E. La Berge (now of the University of Nebraska, Lincoln, Nebraska), Ellen Ordway of the University of Kansas, Carl W. Rettenmeyer (now of Kansas State University, Manhattan, Kansas), and Alvin F. Shinn (now of Stephen F. Austin State College, Nacogdoches, Texas).

Dr. David S. Simonett of the Department of Geography, The University of Kansas, kindly visited the main nesting sites and provided the data on soils.

The statistical analyses were done by Miss Ellen Ordway with guidance from Gunther Schlager and F. James Rohlf.

General Account of Lasioglossum inconspicuum

Distribution: This minute greenish black bee, nearly 4 to nearly 5 mm. in length, is widespread over eastern North America, occurring from Quebec to Georgia, westward to Wisconsin, New Mexico, and Texas (Michener, 1951). Over much of this area it is one of the commonest native bees, although so inconspicuous that it is often unnoticed even by entomologists. The species also occurs in the vicinity of Riverside, California, where it was presumably introduced from the eastern or central part of the United States.

In eastern Kansas, where our observations were made, the species is generally distributed. It is sometimes very common and can be taken at least occasionally on almost any clump of suitable flowers. In this area trees and bushes cover most of the noncultivated terrain and the average rainfall is relatively high (35 inches annually at Lawrence). In central Kansas (area of Caldwell, Hutchinson, and Salina), however, the rainfall is less and uncultivated land is largely treeless except in stream valleys. In this area *L. in-*

conspicuum is largely confined to stream valleys although other species of its subgenus are common in the drier uplands.

Although *Lasioglossum inconspicuum* is found in an area most of which was once deciduous forest, it is not a bee of forests themselves. It usually nests in exposed bare soil, as will be discussed in detail in the section on "Distribution of Nests," and we have never found it burrowing in the forest floor. Originally the forest margins and perhaps occasional bare streamside areas must have been its chief habitats. Destruction of forests, overgrazing of pastures, erosion of soil and development of brushy or weedy wastelands must have enabled the species to become much more abundant and possibly more widespread than in primeval times.

Life History: A brief account of the life history of *L. inconspicuum* is given here to provide background for subsequent sections of the paper, where most of the matters mentioned will be treated in greater detail. The bee is social to the extent that its nests, which are burrows in the soil, are usually occupied by several females. One or more of these is a queen, the others workers, but these castes are very similar and overlap broadly in size. Without information as to season, young females can be placed as to caste only if unusually small (workers) or large (queens). The caste of older individuals (with worn mandibles) can be determined more readily when ovarian development and spermathecal contents are considered.

The species overwinters as adult fertilized queens in the nests. In the spring these queens provision cells and lay eggs, either in new nests or in the old ones. The cells are mass provisioned and usually closed after the eggs are laid, as in most other halictines. After preparing about five cells, the queen ceases her activities until these progeny reach maturity. All of them are workers. They deepen the nest and provision other cells in each of which the queen lays an egg. From this time on the nest is usually continually active, there being no separated broods as in the European *L. malachurum*. The short-lived workers are replaced as they die so that several of them are ordinarily present in the nest. The queens probably are sometimes replaced during the summer, and some males are produced during that season. In fall queens and males are produced in the nests, and it is these young queens which pass the winter.

Seasonal Cycle[1]: Overwintered queens were first seen in the

1. Numbers in parentheses in this section indicate the number of years when appropriate observations were made.

spring at Lawrence, Kansas, on various dates from March 25 to April 16(6). Three of the six early spring records are in the first week of April. Each of the early records is based on an observation of bees flying about or alighting on the ground, but without any evidence of excavation of cells or other work in the nest. Tumuli (piles of excavated earth) at the nest entrances or regular going in and out of well rounded nest entrances were first noted on dates ranging from April 3 to 26(6). The first queen seen carrying a pollen load into the nest (*i. e.,* the first evidence of provisioning of cells) was observed on dates ranging from April 13 to May 1(7).

The first bees recognized as workers, either by dissection or by augmentation of nest populations, were noted on dates ranging from May 31 to June 10(5). Males were first seen, always in small numbers (usually only one or two in hours or days of observation), on dates ranging from June 1 to June 18(5). Because males might be produced as a sort of abnormality in nests that had lost their queens, and because the records in the first half of June may represent the parasitic species, *Lasioglossum cephalotes,* it seems worth noting that our earliest excavations of male pupae from nests which also contained female pupae were from June 20 to July 8(3). Since we dug relatively few nests, about 40 during June, compared to the total numbers of nests in the areas studied, it is not surprising that males from one or another nest would be seen in flight before any male pupae were found in nests. We therefore cannot be sure of the significance of the late dates for the male pupae. We did dig one nest containing male but no female pupae on June 17.

The last females, presumably workers, were seen carrying pollen on dates ranging from August 28 to September 13(4) and very few cells are provisioned as late as these dates. The last overwintering queens were seen in flight from October 1 to 22(4); the last males from September 26 to October 12(3). Overwintering queens were seen guarding nest entrances as late as October 10 to 22(3).

Natural Enemies: Lasioglossum (Chloralictus) inconspicuum is frequently parasitized by *L. (Paralictus) cephalotes* (Dalla Torre). A later paper will concern the biology of this parasitic species and its relations to its various hosts, all of which are in the subgenus *Chloralictus.*

A small mutillid, *Pseudomethoca frigida frigida* (Smith) (det. K. V. Krombein) is common in and about the nests of *L. inconspicuum.* It has not actually been reared from cells of this bee. [We have also taken it in the nests of *Lasioglossum zephyrum*

(Smith), *rohweri* (Ellis), and *versatum* (Robertson) and in nests of *Augochlorella striata* (Provancher).]

We have reared males of a minute tiphiid, *Myromosula parvula* (Fox) (det. K. V. Krombein), from their cocoons in cells of *L. inconspicuum* and have captured a few females in the nests of the *Lasioglossum.*

Female (but not male) Strepsiptera (*Halictoxenos*) are occasionally found in abdomens of *L. inconspicuum,* as are larvae which appear to belong to the Conopidae (Diptera).

Except for the forms listed above, natural enemies in nest of *L. inconspicuum* are not noticeable. Some cells are destroyed by mold, but there is always a question as to whether this is a primary enemy or merely attacks already dead eggs or larvae, thence spreading onto the pollen mass.

Outside the nests, of course the adults are subject to the usual predators.

Activity Outside the Nests

Conditions for Outside Activity: Detailed data on temperature, light, wind, and other factors associated with flights from the nest have not been obtained, as other data seemed more important. However, the meager information obtained is perhaps worth recording. Except as otherwise indicated, temperatures were taken in the shade of the observer's body 30 cm. above the ground. At 50° F. no bees were seen. At 62° F. guards were seen in some nests, but no flights were made. Pollen-collecting flights were observed at temperatures ranging from 70° to 105° F. Of course temperatures at the soil surface are much higher in direct sun light, and as will be explained in more detail in the section on "Guards," the guards withdraw from unshaded nest entrances when the temperature obtained by laying a thermometer on the ground surface in direct sun light reaches about 125° F.

Of course strong wind usually results in reduced activity, but pollen collecting flights sometimes occur when a warm wind is blowing so strongly that the bees are rolled over and over on the ground if they alight in approaching the nest. At such times bees may cling to weeds and leaves, and several may then enter a nest in quick succession when there is a lull in the wind.

Hours of Activity: The time of day when activity begins varies with the season. On various clear days in June, the first flights from nests in the morning were observed from 6:40 a. m. to 9:00 a. m.; on

cloudy days the first flights were later. In the afternoon, a bee was seen to leave the nest as late as 4:55 p. m.

It is a common observation of persons collecting bees about flowers that, except on the hottest days, collecting is best in late morning hours. As a biproduct of observations of the activities of marked bees, we obtained numerical verification of this collector's impression. Figure 1 shows the number of worker bees entering at different times of the day into nests that were under observations. The maximum was reached during the period from 8:30 to 11:30. Our data were largely gathered during hot summer days; this may explain the relatively early maximum. Afternoon activity was about half of that in the morning. Separate lines for bees returning to the

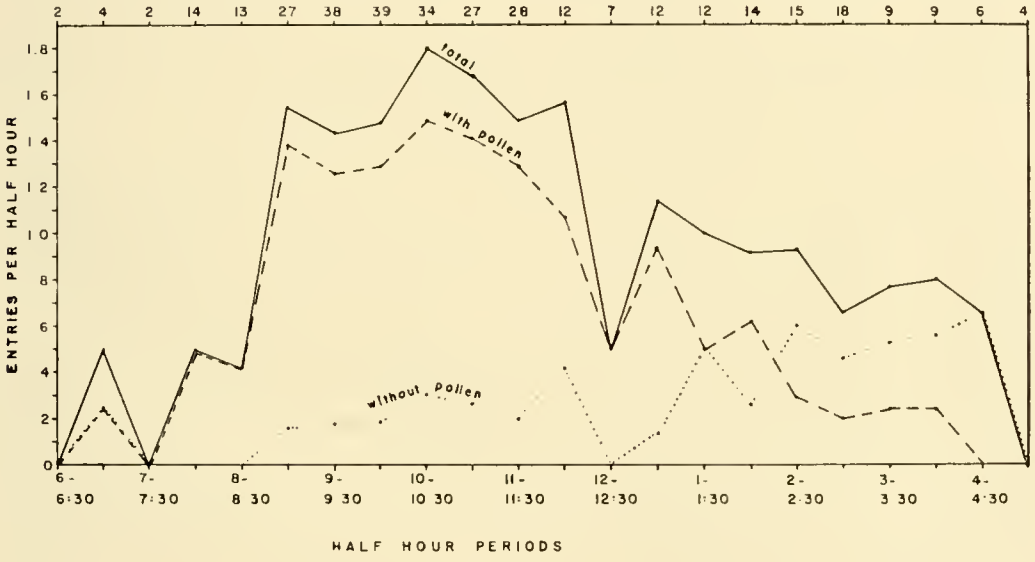


FIGURE 1. Graph showing the average number of times per half hour period that females (probably all workers) entered their nests after trips afield. All observations were made during the months of June, July, and August. The figures across the top of the graph show the number of half-hour periods during which nests were under observation; irregularities in the early morning are doubtless due to the small number of observations. The *solid line* indicates the total average number of entries. The nests studied were usually the most active ones available, so that the figures are strongly biased upward. The *broken line* shows the average number of entries of bees with pollen loads on the legs. The *dotted line* shows the average number of entries of bees without pollen loads. The total is sometimes higher than the sum of the other two, since bees sometimes got into their nests without our determining whether or not they were carrying pollen.

nest with and without pollen loads on the scopa show pollen collecting to be the dominant outside activity in mornings but flights presumably for nectar gathering or probably merely for feeding of adults increase through the day (except for a midday lull) and are the dominant outside activity in late afternoon. We know from observations of bees marked for individual recognition that at least

some of the afternoon flights from which bees returned with no pollen loads were made by individuals which had collected pollen earlier in the day and did so also the next day.

There is no reason to believe that the reduced afternoon activity is due to poorer weather in the afternoon. The observations were made during 50 different days scattered through three summers. The reduced activity may be related to reduced availability of pollen because it is utilized by bees during the day, but some individuals were able to obtain pollen loads in short periods of time in the afternoon and the average duration of pollen-collecting trips was not longer in the afternoons than in the mornings. It seems likely that an innate feature common to the activity of most bees is the tendency, in fine weather, to do more foraging in the mornings than in the afternoon. Scattered data on other species suggests that the afternoon increase in trips for purposes other than collecting pollen is also a common tendency at least among halictines.

Flowers Visited: Like most halictines, *Lasioglossum inconspicuum* is polylectic, that is, it visits and even collects pollen from a wide variety of flowers. Polylecty is a usual characteristic of social bees; since such bees are active through a long season, no one flower is ordinarily available to them at all seasons. No serious effort was made to obtain a comprehensive list of kinds of flowers visited by *L. inconspicuum,* since it was felt that almost any flower visited by any bees in our area would be visited at least occasionally by this species. Table I was based upon data on specimens in the Snow Entomological Museum as well as on observations made in the course of the study of this species. Except as otherwise indicated, females or both sexes were found on flowers in the list.

Examination of Table I shows that the large yellow-flowered Compositae (*e. g., Helianthus, Silphium*) so conspicuous in late summer in Kansas are little visited by *L. inconspicuum,* although many other bees, including other species of the subgenus *Chloralictus,* regularly visit these flowers. The selection of flowers is similar to, although more catholic than, that of *Megachile brevis* Cresson (see Michener, 1953) which also uses primarily blue to whitish flowers. *L. inconspicuum* sometimes collects pollen from yellow flowers of *Taraxacum officinale* in the early spring, possibly because there is sometimes a shortage of other flowers at that season.

It is apparent that even in a species of seemingly thoroughly polylectic bee, by no means all of the potential pollen and nectar sources are used. Expressed in different terms, the bees seem to

TABLE I.—List of Flowers on which *Lasioglossum inconspicuum* Has Been Taken in Eastern Kansas. P indicates that females were collecting pollen, S that they were sucking nectar but not collecting pollen. We have no notes concerning activities of bees on flowers not marked either P or S.

Liliaceae		Malvaceae	
Allium sp.		*Callirhoe digitata*	
Gramineae		Lythraceae	
Unidentified	P	*Lythrum alatum*	P
Cruciferae		Umbelliferae	
Sisymbrium sp.?		*Daucus carrota*	
Roseceae		Asclepiadaceae	
Spirea vanhouttei	P	*Asclepias tuberosa*	S
Prunus americana	P	Labiatae	
Fragaria virginiana		*Monarda fistulosa*	P
Malus pumila		Plantaginaceae	
Leguminosae		*Plantago rugelii*	P
Petalostemon candidum		Compositae	
Psoralea floribunda	(♂)	*Taraxacum officinale*	P
Melilotus officinalis	S	*Silphium speciosum*	S
Melilotus alba	P	*Silphium perfoliatum*	
Medicago sativa	P	*Solidago* sp.	S
Cercis canadensis	P	*Aster azureus*	S
Amorpha canescens	P	*Vernonia baldwinii*	P
Amorpha fruticosa		*Erigeron philadelphicus*	(♂)
Anacardiaceae		*Rudbeckia hirta*	
Rhus aromatica		*Echinacea pallida*	
Rhus copallina	P	*Ratibida pinnata*	
Rhus glabra			

have preferences for certain sorts of flowers. Such preferences doubtless occur among most polylectic bees and are responsible for the observation that at a given time different polylectic species often use different flowers in the same area. Such observations are very easily made with various species of *Trigona* and *Melipona* (see Michener, 1946).

Methods of Foraging: Methods of gathering pollen vary according to the flower being utilized as a food source. When working about over the masses of small flowers of *Rhus copallina*, the females can be rather easily seen to brush the anthers with the fore tarsi, to transfer the pollen to the middle legs, and thence to the scopa on the rear legs and probably to the hairs of the abdominal sterna. There is no regular timing of the movements, nor is there regular alternation of the movements; that is, sometimes pollen is trans-

ferred backward twice in succession on one side of the body before the same action occurs on the other side.

It seems that basically similar actions are used for collecting pollen on other flowers, but the modifications resulting from different flower structure are great. For example, to gather pollen from the flowers of *Plantago rugelii*, the bee alights on the long stamens, and as she hangs downward she clasps several of them together with the hind legs, then brushes pollen off of the anthers with the forelegs, transferring it backward to the scopa by the process already described. The bee flies from place to place on the flower mass; walking among the stamens looks to be impractical. It appears that pollen gathering must vary greatly in efficiency on different flowers.

Observations of pollen collecting bees in areas of mixed flowers showed that on any given trip a bee usually gathered pollen from a single kind of flower instead of going to various kinds and obtaining mixed pollen loads. Observations of marked bees going in and out of a single nest often showed that they were collecting from different flowers. For example, one might bring in loads of yellow pollen while another was bringing white. Moreover, a single bee might change the type of pollen it was gathering, so that after a yellow load, she might bring a white one.

Sometimes bees collecting pollen may suck nectar from another flower, then go on collecting pollen from the first. For example, a bee was seen collecting pollen of *Plantago*. She then flew to *Melilotus alba*, sucked some nectar, and returned to collecting pollen on *Plantago*. *Melilotus alba* is sometimes used as a pollen source, although perhaps not when *Plantago* pollen is also available.

Sometimes bees are seen to return to the nest with only a light dusting of pollen on the scopa. Presumably such bees were gathering nectar or feeding and in brushing among anthers, some pollen adhered to their hairs. What becomes of such pollen is quite unknown.

In late fall, after most of the flowers have disappeared, overwintering queens sometimes feed on honeydew. Details of this will be given in the section "Behavior of Queens."

Activity Around the Nests: Most of the activity of female bees around their nests has to do with coming and going of the bees. Bees leaving the nests often fly directly and promptly away from the nest entrance. Sometimes, especially in cool weather or in the early morning, bees come out of the hole very slowly, turning the

head jerkily from side to side, often lingering half exposed for some seconds, and may crawl as much as a centimeter from the hole before flying. In flight, the departing bee may dart away with very little "orientation flight" over the nesting area. This is particularly characteristic of departures occurring during the heat of summer days. On cooler days and in early morning hours, it is more common to see irregular zig zag or sometimes spiral "orientation flights" as bees leave. Such a flight requires up to 15 seconds, and during it the bee rises to a height of some four centimeters above the ground surface, flying about over an area of up to 30 cm. in diameter, although usually smaller, before making off. Figure 2 illustrates some flight patterns of bees leaving nests.

FIGURE 2. Flight patterns of females leaving nests. The lower one represents an unusually extensive "orientation flight."

The more elaborate and prolonged forms of departure mentioned in the preceding paragraph are characteristic, often in exaggerated form, of young adults. We noted this on several occasions, when activities of marked pollen collectors were being observed day after day. As unmarked bees began making trips from such a nest, they almost always made more elaborate departures than the presumably older, marked, foraging bees leaving the nest at the same time. A few days later the unmarked bees were seen collecting pollen and making the usual quick departures.

Bees accustomed to the nest usually fly almost directly to it, zig zagging only slightly in the last few centimeters of the approach to the nest. They alight almost at the threshold of the hole and quickly crawl in. Queens going into their nests in spring, and young females at other seasons, often seem to have difficulty finding their nests. They may alight on the ground near the nest, and after walking about, even starting to dig, they fly again, often repeating the performance for 15 or 30 minutes until they ultimately find the nest entrance. It seems apparent that such bees have little difficulty in getting within about half a meter of the nest, but the exact location of the nest seems often to be discovered by chance. Of course the number of such disoriented bees is greatly increased by any disturbance of the soil surface, such as trampling by cattle or persons, which may occur while bees are afield.

Occasionally disoriented bees enter the wrong nest, but usually soon leave again. The probability exists, however, that they may sometimes become incorporated into the populations of other nests as suggested by the results of the experiments on transferral of young workers from nest to nest, as described in the section on "Behavior of Workers."

Collections of disoriented or lost bees in locations where no surface disturbance could account for disorientation revealed not only young bees with unworn mandibles, as would be expected from the preceding paragraphs, but also some bees with much worn or very much worn mandibles. Presumably these are senile bees; the few dissected have all been workers. Like the unworn ones they give every impression of looking for their nests, examining every little hole, sometimes starting to dig, but soon walking or flying on. Such lost bees sometimes go away from the nesting area for half an hour or more, then return and resume their searching. We have marked such bees with paint and found them still searching the next day. We presume that some senile bees lose their ability to

return to their nests. In two cases which we observed, lost bees were individuals that had been previously marked and their activities observed in certain nests. In both cases the nests were seemingly normal, and exhibited normal activity, while the disoriented senile bees searched within a meter or two of their nests.

Duration of Trips and Periods Between Them: The data on this subject were obtained by means of bees marked for individual recognition. Most of the data were gathered from marked workers, but queens in the spring, when they are provisioning cells, make trips of similar duration and similar variabilty in duration. The information on queens has therefore been lumped with that obtained by observing workers, and is presented in Figure 3.

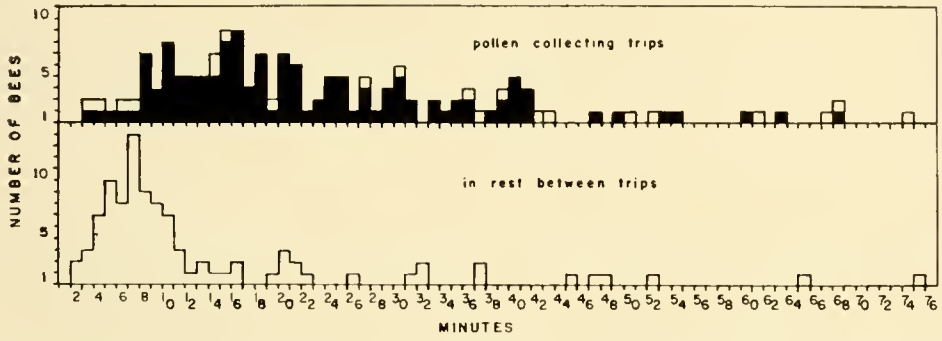


FIGURE 3. Histograms showing (above) durations in minutes of trips away from nests, black areas indicating that the bees returned to the nests with a pollen load on the scopa, and (below) durations of periods that bees spent in the nests between pollen-collecting trips.

Because pollen-collecting bees usually enter and leave their nests rapidly, it was found difficult to sit beside one or two nests and record every entry or departure. Sometimes bees would be missed altogether; more often they would be seen but their color markings could not be recorded with certainty. To slow down the bees entering the nests, we often put a straw or grass blade across the nest entrance. The resultant delay enabled us to record the color combinations of entering bees, but did not help with the departing individuals which would crawl from beneath the obstruction and immediately take wing. Therefore we have over one hundred records of the period from a time when a bee entered her nest until the next time that she entered her nest. These data support the picture indicated by Figure 3. In two cases the period from one entrance to the next was over 200 minutes.

We have records of trips from which bees returned with pollen loads on the legs ranging from 3 to 105 minutes in duration. As shown in Figure 3 the bulk of such trips take from 8 to 40 minutes,

with the maximum number of trips requiring about 16 minutes. The great variation in duration of trips may be due to variations in the ease with which pollen is obtained. There is some tendency for a series of successive trips by a single bee to be of about the same duration, as shown by this example (time given in minutes, P signifies return with pollen load): 13P, 24P, 13P, 15P; another example, 8P, 9P, 9P. However, durations of successive trips may vary strikingly, as shown by the following series: 36, 40P, 15P, 11P and 15P, 14P, 8P, 5P.

Successive periods spent in the nest between trips often vary considerably, as shown by the following five series (given in minutes): 4, 5, 5; 6, 2, ?, 6; 3, 2, 4, 9, 7; 8, 31, 9; 6, 7, 16, 37. As shown by Figure 3, the range of variation is far less than for trips afield. In the case of the last series shown above, the 37 minute stay in the nest was due to the bee spending a considerable time as a guard before leaving on the last trip.

These data in general show rapid trips and in theory a bee ought to be able to make many trips per day. As shown in Figure 1, however, outside activity of all sorts and pollen collecting trips particularly, diminish in the afternoons. The largest number of pollen collecting trips that we have ever seen a bee make in a day is seven. We often watched nests until activity seemed to have ceased for the day, and we are confident that more than seven trips per day would be unusual.

By no means all of the bees in a nest that are apparently able to collect pollen actually do so actively at any one time. This is shown in Table II, which shows the number of pollen collecting trips made by various workers during periods of three hours. As indicated by the zeros, a considerable number of workers made no trips whatever. Some of these were presumably young adults not yet ready to undertake foraging activities but others had been seen returning with pollen on previous days. It is also evident from Table II that many make only one or two trips during the time that others make five or six. The trips of the bees making few trips take no more time, on the average, than those made by bees making more trips. Rather, the bees making few trips seem to start late, stop early, or both, thus spending much more time in their nests.

In connection with the above paragraphs it should be mentioned that the data were collected from some of the most active nests and on days of great activity. The majority were less active, and nests like nest 1, Table II, which showed no activity in three hours, were common.

TABLE II.—Number of Pollen Loads Carried into Nests by Individual Bees During Periods of Three Hours Duration. Opposite "Number of Workers" is indicated the number of workers (marked for individual recognition) known to be present in the nest on the day when it was observed continuously for three hours. Opposite and below "Number of pollen loads" is indicated, for each worker, the number of loads that she carried into the nest. Data from different nests or different days are separated in lettered vertical columns. All data were gathered during the morning hours, *e. g.*, 8 a. m. to 11:00 a. m. or 9:00 a. m. to 12:00 a. m., during the months of June, July, or August.

Nest	a	b	c	d	d	e	f	f	g	h	i	j	k	l
Number of workers	8	8	7	7	7	7	6	6	6	5	5	5	4	4
Number of pollen loads for each worker (Most active foragers above, least active below)	6 5 3 2 1 1 0 0	5 2 1 0 0 0 0 0	4 4 2 1 1 0 0	2 1 1 1 0 0 0	3 3 1 0 0 0 0	4 1 1 0 0 0 0	2 1 1 0 0 0	3 2 0 0 0 0	3 2 2 1 0 0	4 4 0 0 0	3 2 1 0 0	1 1 0 0 0	6 2 1 0	0 0 0 0
Total pollen loads	18	8	12	5	7	6	4	5	8	8	6	2	9	0

Variability in activity among nests is the rule rather than the exception. For example on July 3, 1952, three nests within 10 cm. of one another at Engle's Place were observed all day. In one, six different marked bees were seen at the entrance or going in and out, some of them busily carrying pollen. In another nest, two bees were seen, one of which made one trip afield. In the third nest, only a guard was seen, and she never left the nest. Such diversity is associated with varying nest populations resulting in part from variations in the number and activity of queens. In a population in which many colonies are dying throughout the year, one must expect to find many nests which seem inactive because of dwindling populations. However, we often also found relatively inactive colonies which later became active, presumably because of emergence of additional workers.

Probable Lack of Social Facilitation: Observers watching nests of *L. inconspicuum* (as well as other colonial halictines) are often impressed by the fact that there seems to be a tendency for several individuals to leave a nest or return to it in a short space of time. It sometimes happens that after watching a nest for many minutes and seeing no activity, an observer sees several bees leave within a period of five or ten minutes.

To determine whether there was social facilitation so that departure of one individual tended to be associated with departure of others, departures as well as arrivals during nineteen morning periods of good weather ranging in length from 60 to 190 minutes were tabulated. The observations were made at various nests and during all the summer months. The periods of observation were divided into ten minute units. There were 179 such units during which bees leaving the nests had been noted and 162 when bees entering nest had been recorded. During about 150 of the periods both arrivals and departures were recorded; during the remainder only departures or only arrivals were noted for one reason or another. The results of this study are shown in Table III. It can be seen that for both entering and departing bees, the frequencies of two or more per ten minute period exceed the frequencies expected from the Poisson distribution. The differences from the Poisson distributions are not satistically significant, however, for departures and are scarcely so ($.02 < X^2 < .05$) for arrivals. The consistency of the differences for the two sorts of data (arrivals and departures) suggests that they may not be mere sampling errors. They might result from external factors (a cloud over the sun or the presence

TABLE III.—Numbers of Females Entering or Leaving Nests During Ten Minute Periods. Most of those entering carried pollen loads on their legs.

Bees per ten minute period	Observed and expected frequencies			
	Entering		Departing	
	Observed	Expected	Observed	Expected
0	60	59.60	70	72.78
1	54	59.60	64	65.50
2	31	29.79	30	29.48
3	12	9.93	9	8.84
4	3	2.48	4	1.99
5	2	.50	1	.36
6	.....	.....	1	.05
Totals	162	.....	179	.....

of the observer) holding up departure or return of foragers for a time until several are ready to leave or return at about the same time. Alternatively, guards may sometimes retard departures until several bees are ready to go.

Since the study reported in Table III seemed inconclusive, and since it seemed desirable to relate arrivals at a nest with the departures immediately following them,[1] another study was made, again based on morning observations made during good weather. Because the units of time used were five instead of ten minutes, in length, it seemed reasonable to include briefer periods of observation in the study; twenty-five periods ranging from 40 to 190 minutes in duration were used. Both arrivals and departures were recorded during these periods. The average number of departures for five minutes was determined for each period of observation (Table IV, column 2). If departures were associated with arrivals, then the average number of departures per five minutes following an arrival should exceed the general average number per five minute period. Column 3, Table IV, shows the average number of de-

1. Arrivals of successful forages are related to departures of other foragers in many social insects, such as *Apis, Trigona, Melipona, Bombus, Polistes, Vespula,* and many ants.

TABLE IV.—Average Number of Females Leaving Nests in Consecutive Five-minute Periods (Column 2) and in Five-minute Periods Starting with the Return of a Bee.

(1) Observational period	(2) Mean number of departures per five minutes	(3) Mean number of departures in five minutes following arrivals	(4) Duration of observations (minutes)
1	.15	0	100
2	.17	0	90
3	.20	0	50
4	.25	0	40
5	.27	.33	75
6	.28	.25	70
7	.29	.67	70
8	.30	.09	185
9	.31	.70	145
10	.31	.83	145
11	.36	.40	140
12	.36	.35	100
13	.36	.22	100
14	.36	.67	95
15	.39	.58	190
16	.44	.80	45
17	.49	.52	185
18	.55	1.00	110
19	.58	.50	155
20	.60	.86	50
21	.76	.33	75
22	.78	.67	45
23	.85	1.23	65
24	.88	2.00	40
25	1.13	1.00	75
Mean	.46	.56	

partures in five minute periods, each of which starts at the moment of arrival of a bee (almost always a pollen-laden forager).

Examination of Table IV, in which the observational periods are arranged in order of increasing mean departure rate, shows that when there is little activity, the few departures seem to have little relation to the arrivals. At low departure rates, assuming no relation between an arrival and the ensuing departure, it is not surprising that the departures commonly fall in the long intervals

between arrivals. When there is more activity in nests, the number of departures per five minutes following arrivals clearly exceeds, in most instances, the mean number of departures per five minutes. At first thought this would seem to indicate some sort of social facilitation in which the return of a forager stimulates the departure of others, acting either through the guards or directly upon other foragers. This is apparently not true, however, for Figure 3 shows that some 28 percent of the periods between trips by a given forager are five minutes or less. Excluding first trips for the day, this percentage of the departures is in reality associated with arrivals for purposes of the five-minute units used in this study. Therefore it is not surprising that the excess of the mean of Column 3, Table IV over that of Column 2 is 22 percent. In any event this excess clearly does not show an influence of returning foragers on different departing ones.

Lack of social facilitation of foraging trips is hardly surprising in a primitively social form such as *L. inconspicuum* with the nests branched and cells dispersed.

Length of Flights: In early spring when flowers are scarce, one sometimes finds nests being provisioned a considerable distance from any flowers. We have seen such nests as much as 50 meters from the nearest flowers (*Prunus*) that we could find. Presumably the bees fly at least that far.

During the rest of the active season flowers are so generally available that it was never far to them from the nesting sites that we found. We experimented with carrying marked pollen collecting bees away from their nest and releasing them. We assumed that if they found their way back quickly, they were probably familiar with the landmarks at the place where they were liberated. Bees returned promptly from points 75 meters distant from their nest. Unfortunately the experiment was not continued to the point where some of the bees were lost, but it does indicate that in spite of their minute size, these bees fly moderate distances.

NESTS

Distribution of Nests: Nests have been found in the soil of a wide variety of sunny or partly sunny locations. Undoubtedly many of the nests are isolated. Because of their inconspicuousness, solitary nests are difficult to find. We came upon them occasionally, however, in overgrazed pastures, parkings or partly bare areas on the University campus, along an abandoned road, etc. Those that

we studied or excavated seemed quite comparable to nests in aggregations.

It was convenient for us to make our studies in places where we could find numerous nests in the same vicinity. Fortunately several such locations were found, after much and often fruitless searching, in the vicinity of Lawrence, Kansas. The accounts of these places below give some idea of habitats in which *Lasioglossum inconspicuum* nests. The locations are sufficiently variable that we have never been able to learn how to recognize a nesting area from a distance. This is because of the great amount of ground seemingly similar to that of the nesting aggregations, and yet without nests or with only widely scattered, isolated ones.

Even in the aggregations, the nests were not closely placed. In late spring, when the number of nests is at its maximum, there were occasionally found places having perhaps ten nests in an area of one fourth square meter. These were exceptional local concentrations within larger aggregations. By midsummer or fall most of the nests established in spring are dead, and often there was only about one nest per square meter in the aggregations. The aggregations are loose and usually lack definite margins because with careful searching scattered nests can often be found in the surrounding areas.

The nine aggregations from which we obtained nearly all of our data on *Lasioglossum inconspicuum* are briefly described as follows:

1. *Potter's Lake.* This is on the campus of the University of Kansas. The nests were found along a slightly sloping path which received considerable use. Although a few isolated nests were found from time to time elsewhere along this path, most of them were in an area about 10 meters long and 2 meters wide. Scattered plants of bluegrass (*Poa*) and plantain (*Plantago rugelii*) grew in and especially along the sides of the path. The nests were often found among these plants as well as in areas of bare soil. Large trees (elm and hackberry) shaded the path except during four or five midday hours. In one area where new nests were established each spring before leaves grew on the trees, shade continued nearly all day when the trees were fully leaved. In this shady place nests died out in early summer. The mortality of nests elsewhere was so high, however, that one could not be certain of the effect of shading on survival of the nests. The soil was hard and rather crumbly when dry, with considerable amounts of clay. The surface was often dusty due to foot travel along the path. It

was in a low area, however, and remained moist longer than soil of the hill tops.

Among nests of *L. inconspicuum* at Potter's Lake were numerous nests of *Andrena erythronii* Robertson (area II of Michener and Rettenmeyer, 1956) and during the earlier years of observation, *Calliopsis andreniformis* Smith. Other bees nested in the area only occasionally.

2. *Cooper's Place.* There were two sites grouped together under this name in a little used pasture about nine miles southeast of Lawrence. They were on nearly flat but well drained ground, and were in small areas of short sparse grass where the soil surface was exposed to the sun. Each of the areas was about five meters across. There were no nearby trees or large bushes to provide shade. The main vegetation outside the immediate areas where the nests were found consisted of *Symphoricarpus orbiculatus* and *Rhus copallina.* The nests were in surface soil of Dennis Fine Sandy Loam, developed on sandstone.

In one of the two areas in the pasture, enormous numbers of nests of *Lasioglossum (Chloralictus) rohweri* (Ellis) occurred in 1951, but not in subsequent years. A few nests of *Augochlorella aurata* (Smith) and *A. striata* (Provancher) also were found in the same area.

In the spring of 1957 the pasture was plowed and sown, destroying it for the time being as a nesting place.

3. *Engle's Place.* The nesting area called by this name consisted of some nearly bare areas sparsely inhabited by *L. inconspicuum* in an overgrazed pasture about eight miles southeast of Lawrence. The ground was gently sloping, well drained, and high enough to be quite dry. The vegetation was sparse; aside from scattered trees of hedge apple (*Maclura pomifera*) which did not shade the nesting areas, the principal vegetation was weeds such as *Vernonia baldwini.* The soil was like that of Cooper's Place.

In the spring of 1957 the area was plowed, destroying it for use by *L. inconspicuum* as long as cultivation is continued.

4. *Intersection* (Figure 40). This area was on a dry, rocky hill about nine miles southeast of Lawrence. The ground in the nesting area was flat. It was protected from grazing and had never been cultivated, but had been much disturbed because it was on the former site of a schoolhouse. Perhaps because of its rockiness, vegetation was not everywhere dense; there was an area about

six meters square largely occupied by sparse vegetation so that the soil surface was largely exposed. There was no shading by bushes or trees. In this area the principal plants were tall grasses and *Verbena stricta*. Outside of the nesting area the same plants, together with *Rhus copallina* and others, formed dense masses which made the ground there unsuitable for nesting of *L. inconspicuum*. Because of removal of the surface soil at some time in the past, the nests were in subsoil of Dennis Fine Sandy Loam, developed on sandstone.

A few nests of *Halictus confusus* Smith were found in the same area.

5. *State Property*. The area called by this name was about two miles southwest of Lawrence, on a gentle slope. Although not cultivated for many years, if ever, native vegetation was entirely gone and replaced by weeds. Hedge apples (*Maclura pomifera*) were nearby trees, but did not shade the nesting area. The nesting area itself was sparsely covered with grass, unlike much of the adjacent ground which was densely weedy or grassy. The soil was Newtonia Silty Clay Loam developed on Oread Limestone. The nests occurred in a space of about four square meters and were associated with burrows of *Augochlorella striata* (*Provancher*) and *A. aurata* (Smith).

After 1955 no nests of *Lasioglossum* were found in this area, probably because the grass became dense in the nesting place.

6. *Sycamore Slope* (Figure 38). This area, on the University of Kansas Natural History Reservation, was in ground cultivated at one time, but since 1946 it has been sown with native prairie grasses and left strictly alone. The nests were on the sides and summits of some small bare ridges resulting from erosion. The nests were found in an area about three meters on a side. There was no shade. Nests of *Augochlorella aurata* (Smith) and *striata* (Provancher) were associated with those of *Lasioglossum*. Another area in which we found some nests was along the side of the road near the main sycamore slope area. Both of these places are upland areas of severely eroded Pawnee Silty Clay Loam developed on glacial drift.

7. *Prairie Road* (Figure 39). This was on another part of the University of Kansas Natural History Reservation. An abandoned road (merely a pair of wheel tracks) crosses few acres of upland prairie that has never been cultivated. In one section of this road, about seven meters long, nests were found in considerable numbers

both in the exposed soil and along the edges of the tracks where they were largely shaded by overhanging prairie plants. Elsewhere along the same road across similar soil, there were only occasional isolated nests. Vegetation consisted of typical prairie plants with some intrusion of *Rhus copallina*. The soil at this location was a Newtonia-like Silty Loam developed on limestone.

8. *Petefish's Place.* The nests at this location were in a level area about three meters square of mixed sand and clay along a stream five miles southwest of Lawrence. The location was so low that it must have been flooded most years; flooding was shown by the bent grass and drift wood at the time of our work in this area. The surface was bare except for scattered clumps of grass and of sweet clover, *Melilotus alba*. The area was exposed to the sun most of the day but was shaded in the later parts of the afternoons by elms, hackberries, and other trees. The soil was a sandy loam, quite loose and obviously more sandy than at any other location where this species was studied.

9. *County Line:* This was an overgrazed upland pasture along the Douglas County-Franklin County line south of Lawrence. There was sparse grass and abundant weeds, such as especially *Vernonia baldwini*. The nests were widely scattered in small bare areas in the pasture. There was no shade except that afforded by the grass and weeds.

Common Features of Nesting Areas: From the descriptions of nesting areas given above it is possible to extract some common features which are presumably necessary for nesting by this species. The soil surface is flat or gently sloping in all cases. It must be exposed; no nests were found where the soil was densely covered by vegetation (as on undisturbed portions of prairies or in densely weedy areas) or by fallen leaves (as on the forest floor). The nesting site is typically exposed to the sun all or most of the day. Nests started in the spring under deciduous trees disappeared after the foliage cast its shade. The soil was in all cases loam, usually surface soil but sometimes subsoil. The soil may be derived from sandstone, limestone, or glacial drift. Nesting may occur in prairie soil disturbed only by removal of vegetation or in areas that were once plowed and have been severely eroded or even in streamside sandy loam deposits. In spite of all this variation in soils used, the material is always compact and often hard; nests never occur in loose sandy soils. Nesting may occur in stony situations where nests must curve around the rocks or penetrate them if not too

hard. Nests may be found on hilltops, slopes, or in stream valleys. As explained in the section on "Survival of Nests" below, we think that lack of moisture in soil sometimes results in death of colonies of the bees.

Because of destruction of natural forests and prairies, heavy grazing, and sheet erosion, very numerous areas provide the requirements for nestling noted above. Some possible reasons for development of aggregations will be discussed in the section on "Distribution of Nests."

Differences in Activities Among Nesting Areas: Differences in activities among the various nesting areas were often noted. Thus in late May and early June, 1952, we noted that some nests at Cooper's Place were still being provisioned by the founding queens, that there were no smooth areas around the nest entrances nor were there guards, and that most of the nests were closed and unrecognizable. At the same time at Potter's Lake many of the nests had already produced workers which guarded the well-formed entrances and made smooth areas around them; queens were probably rarely seen at the surface of the ground. Not until June 5 did these features appear in the Cooper's Place population.

Later we noted that guards in the nests at Cooper's Place appeared to be timid and disappeared into their nests at the slightest disturbance; only rarely would they turn and block the entrance with the abdomen and then only well down below the surface of the soil. At Potter's Lake the guards were much less easily disturbed, and when disturbed they readily turned and blocked the entrance with the abdomen, doing so close enough to the surface that they could easily be marked with paint for individual recognition while in this position.

On July 5, 1952, we noted that colonies at Potter's Lake and Cooper's Place had been inactive for several days, possibly because of prolonged dry, hot weather (reaching 39° to 41° C. daily in shade), but colonies at Petefish's Place remained active, possibly because of the low, cool location near a stream.

In examining nests in different locations, we found that there is a strong tendency for nests in any one location to be similar in depth and form. This is probably because of differences in soil (including soil moisture) in different places. For example, in midsummer, nests at Cooper's Place tended to be deep (usually over 65 cm.), and little branched except at the lower levels where there were cells. At the same season nests from Potter's Lake were rarely over

60 cm. in depth, usually shallower, and often rather broadly branched even at the upper levels.

These examples illustrate the danger of generalizing from nests observed in only one location or for only a brief period.

Survival of Nesting Aggregations: As already indicated, several of the areas described above were occupied by nests of *L. inconspicuum* over a period of several years. The site at Potter's Lake had nests in it every year of our study. Sometimes in late summer there were only one or two nests known to us in the area, but each spring a new lot of overwintered queens established nests there. At Cooper's Place, one of the areas had nests for only two years but the other was occupied each year until it was plowed in 1957. Sometimes in late summer or fall not one nest could be found in the area, but in spring it was always reoccupied. Similar observations were made at other areas of aggregation. There was consistently a relatively enormous mortality of nests during each season of activity.

Sometimes, as at the roadside aggregation at Sycamore Slope, although numerous nests were seen in April and May, not one could be found my mid-June. More often a few survived for the entire year. During dry summers we sometimes got the impression that soil humidity was an important factor in nest survival. At the Intersection site, which often became very dry, excavation of nests in August showed that the only ones surviving were those that actually penetrated relatively moist sandstone rock. At Potter's Lake also, one August when but few nests survived, we found that those which we dug penetrated chunks of moist sandstone scattered deep in the soil. These observations, combined with the fact that nests are dug deeper and deeper during the summer at the same time that the soil is becoming dryer, led to our surmise that lack of soil humidity was an important factor in mortality of nests. During the drouth years of 1953 to 56, some of the nest aggregations became entirely extinct, not even being replenished in spring. This occurred at the Intersection, an obviously dry hilltop; at Petefish's Place where the soil became very dry in appearance, probably because of its sandiness, in spite of its low lying location, and probably at Engle's Place. We only have knowledge of Petefish's Place being occupied one summer; it is the most abnormal of the sites found.

During years of adequate and high rainfall many nests also die. We were not, in fact, able to study any nest aggregation for any

season without being impressed at the high rate of mortality for which we have no satisfactory explanation.

The question of the source of the overwintered queens which establish nests in the spring is interesting. There is a surprising number of such bees considering the late spring and summer mortality of nests. Presumably they come from the nests that did survive the summer in the areas of aggregation as well as from the isolated nests. The latter are doubtless far more numerous than out data suggest, for the minute holes in the soil are difficult to find. Among nests excavated in the fall and early winter, the average production of young queens was between six and seven, with a maximum of 18 observed on one occasion. Most of these bees disperse in the spring from their parental nests and establish new ones.

Survival of Nests: Numerous individual nests were marked with numbered nails pushed into the soil a few centimeters from each nest. Each group so marked and used for the present aspect of the study consisted of nests in a single aggregation. The number of marked nests in each group is indicated in Figure 4. The nests were re-examined at daily, weekly, or occasionally less frequent intervals. As will be explained later, nests are often closed temporarily. Colonies were considered as dead only when repeated visits showed a nest to be permanently closed. Excavation of a considerable sample of such nests showed no surviving bees of any

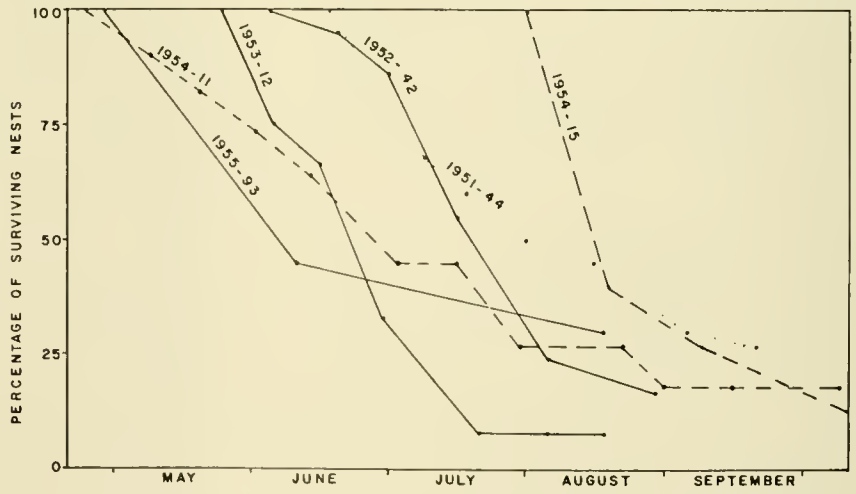


FIGURE 4. Survivorship curves for colonies in six aggregations. A colony was considered dead when its nest became permanently closed. The number of nests in each group is indicated, after the year, along each curve. Each group consisted of marked nests in a single aggregation.

age. Survivorship curves for each six groups of marked nests are shown in Figure 4.

It can be seen that in each group, nests succumbed for a time in such numbers that complete extermination before the end of summer seemed likely. As indicated above, this sometimes happens as aggregations of nests do sometimes become extinct. However, each of the curves shown in Figure 4 flattens out as the season progresses, showing that some nests survived through the summer (or at least until the end of the observations) in each case. Presumably this indicates that a relatively few nests, fortunate in location or in some other attribute, have a good chance of survival while the others die. This means that once a nest survives for a certain time, it has a good chance for longer existence.

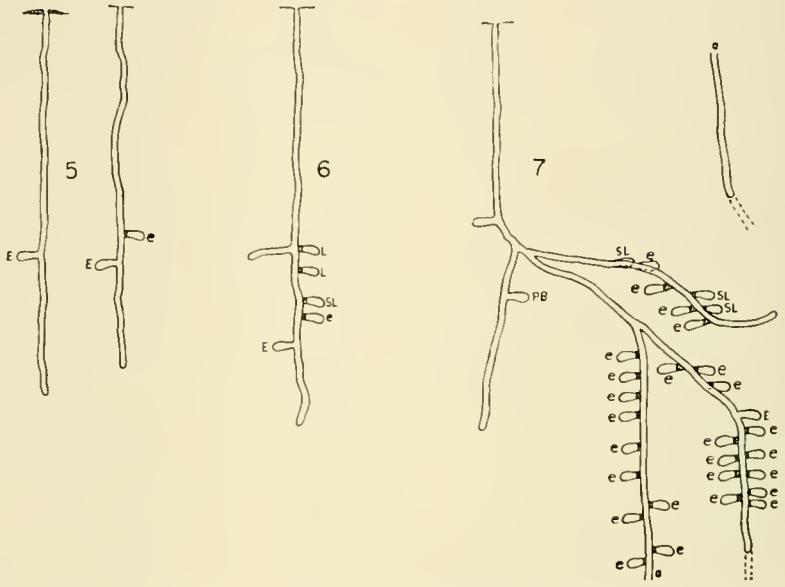
The group studied in 1953 reached a lower level earlier in the season than any of the others. It was at the Intersection, which as already explained was a dry location from which bees ultimately disappeared completely. The groups for 1951, 1952, and the first for 1954 (marked in April) were all at Potter's Lake while that marked in July, 1954 and that marked in 1955 were at Engle's Place.

For the great majority of nests, death of the population was not due to any of the obvious natural enemies (mutillids, *Paralictus*, mold attacking pollen masses). Probably death of the queen and failure to replace her, followed by death of the short-lived workers, was the common cause of extinction.

Nest Structure: The nests consist of burrows which extend essentially straight downward into the soil, but often meander considerably (Figures 5 to 16). In soil full of stones, there are often long horizontal sections following the surfaces of the stones until they reach places where they can go downward. Sometimes burrows, after passing through the soil for some distance, enter sandstone and perhaps other similarly soft rocks; as already suggested such nests sometimes survive better, possibly because of moisture in the rock, than their neighbors entirely in soil. The burrows range from 1.8 to 2.5 mm. in diameter, rarely reaching 3 mm. in diameter in certain parts of the nest. At the surface of the ground the burrows are narrowed to 1.3 to 1.5 mm. in diameter.

Nests made by single queens in the spring have no specialized structure at the surface and the minute holes are difficult to find. Holes occupied by more than one queen in the spring, and those occupied by queens and workers in summer, are ordinarily surrounded by a depressed smooth, shining area (Figure 41) which

appears to be thinly covered by a layer of material of perhaps salivary origin. These depressed areas are 3 to 4 mm. in diameter and the surface is usually horizontal. When the soil is dry they may be poorly kept and may even disappear due to pulverization of the soil but after a rain each active nest will again be provided with such an area. It is only when quite dry that the salivary layer covering the smooth area can be easily detected, for then it pulls away from the soil in places and therefore has a whitish appearance. Rarely in Kansas, we have observed such areas sloping inward, form-



FIGURES 5 to 7. Diagrams of nests. For these figures as well as Figures 8 to 16, several abbreviations and symbols are used. Cells indicated by broken lines are earth-filled. There were often more of these than indicated; and such cells are often omitted even though some were present, for they are hard to recognize unless very freshly filled with earth. The following letter symbols are used in connection with cells: e, egg; E, empty; EF, empty except for larval feces; L, larva of moderate size; LL, large larva and prepupa; M, cell contents destroyed by mold (fungus); P, pupa (all females unless marked male); PB, pollen ball (but no egg or larva); SL, small larva. When diagrams have been broken to conserve space, connecting points are indicated by the same letters.

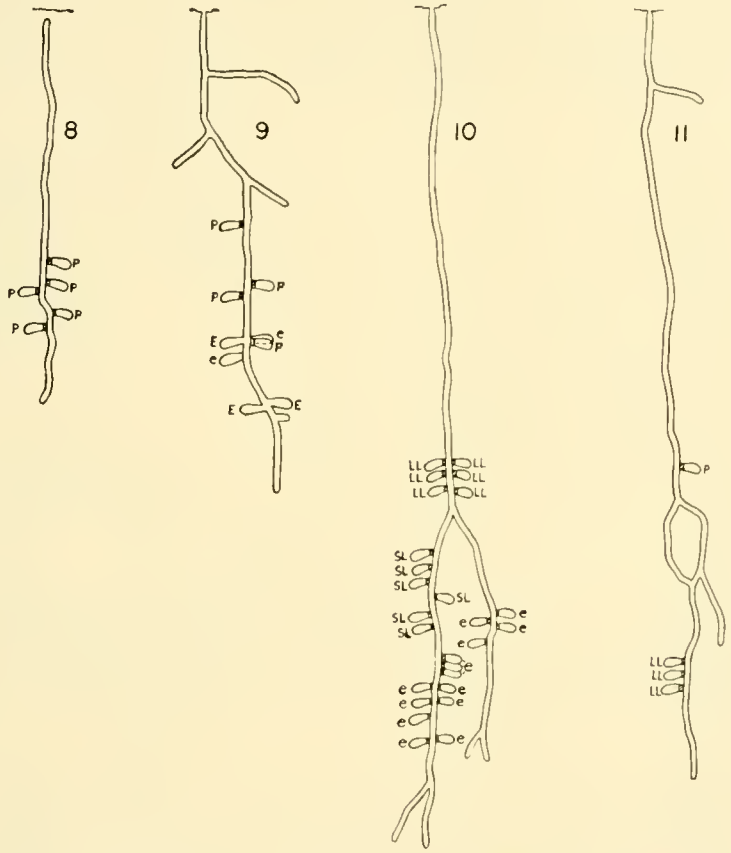
FIGURE 5. Two young queen nests opened on April 27. The one at the left has a fresh tumulus and a single empty cell. Each nest was occupied by a single queen.

FIGURE 6. A queen nest opened on May 6 showing sequence of the brood from oldest above to youngest below. The nest was occupied by a single queen.

FIGURE 7. An old nest opened on April 24 and found to be occupied by a group of four queens which were reusing the burrows of the previous season. Earthfilled burrows extending to deeper levels are indicated by broken lines.

ing small funnels around the entrance holes. One of us (C. D. M.) noted the entrances regularly funnel shaped, sometimes steeply so, at nests of this species in the garden of Mr. P. H. Timberlake at Riverside, California, where *L. inconspicuum* has been introduced from the eastern or central United States. Probably the form is in some way related to the texture of the soil.

When bees are digging, the excavated earth is pushed up to form a tumulus which spreads irregularly around the entrance and reaches diameters of 12 to 18 mm. The material of the tumulus is granular



FIGURES 8 to 11. Diagrams of nests. For symbols see explanation of Figures 5 to 7.

FIGURE 8. Closed queen nest opened for study on May 28. The nest was occupied by a single queen.

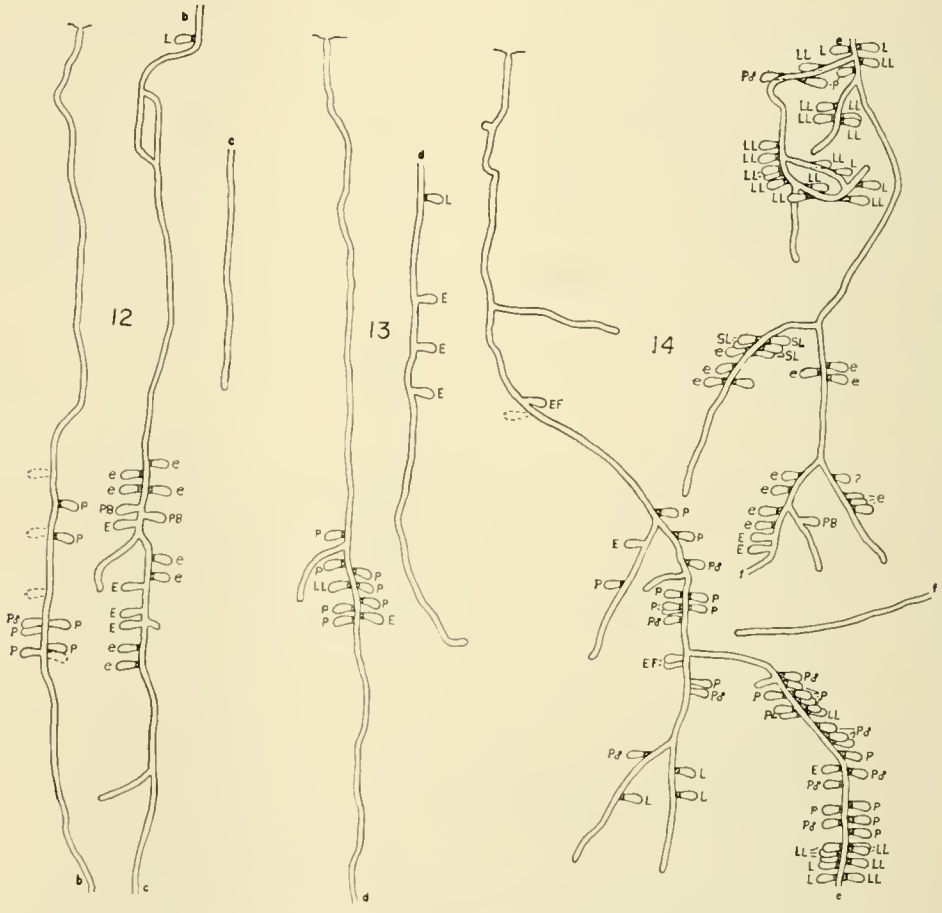
FIGURE 9. Nest opened on June 3. It was occupied by a single queen and two adult workers. Excavation beyond that of a queen nest is shown by the cells containing eggs, by the lower empty cells, and by the partially excavated cell lower than any completed cell.

FIGURE 10. Nest opened on July 16. It contained a queen, two workers, and one bee which escaped.

FIGURE 11. Nest opened on July 16. It contained only one queen and one worker. Obviously the queen had laid no eggs recently.

but often tends to cling together; the bees find their way through it in irregular passages, there is not a uniform passageway through it as is found in some species. The tumulus may cover the smooth area completely. Tumuli, however, are ephemeral structures which wash away in rains or are blown away by winds, leaving the entrances open and surrounded by obvious smooth areas.

We have not noted evidence of burrows being lined with dirt from deep in the nest, as is so often the case among other halictine bees [*e. g., Augochloropsis diversipennis* (Lepeletier), see Michener and Lange, 1959; and *Lasioglossum malachurum* (Kirby), Bonelli, 1948]. The burrows are round in cross-section, not especially smooth walled. Queen nests, established in the spring by single queens, range from

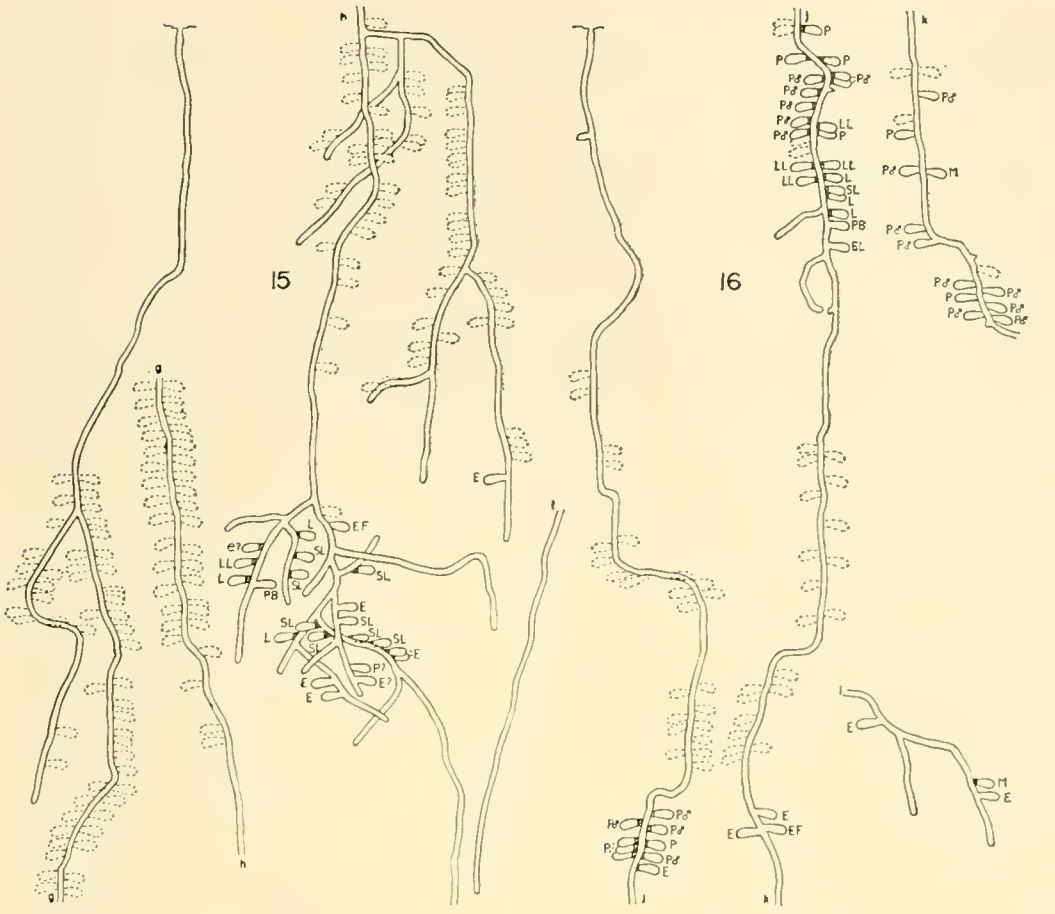


FIGURES 12 to 14. Diagrams of nests. For symbols see explanation of Figures 5 to 7.

FIGURE 12. Nest opened on July 1. It contained one old queen, five worn workers, and eleven unworn females almost all of which were certainly workers.

FIGURE 13. Nest opened on July 2. It contained one queen, five worn workers, and three unworn females that almost certainly were workers.

FIGURE 14. Nest opened on June 26. It contained one little worn queen, eight worn workers, and two unworn females that almost certainly were workers.



FIGURES 15 to 16. Diagrams of nests. For symbols see explanation of Figures 5 to 7.

FIGURE 15. Nest opened on August 4. It contained two queens, twenty workers, and two females of doubtful caste.

FIGURE 16. Nest opened on September 6. It contained one probable worn queen, eight worn workers, and two young females that might well have been overwintering queens.

9.5 to 24 cm. deep and the burrows are little branched (Figures 5, 6, 8, and 9). Nests occupied by two or more queens, usually or always using the burrows of the previous year in which the queens presumably hibernated, are often much deeper, and more fully branched (Figure 7); the deepest that we excavated was 55 cm. deep, and abandoned burrows filled with earth extended even deeper. Lower parts of such reused nests are always partially filled with soil in spring.

With production of workers the nests are extended deeper into the soil, and as shown in Figure 17 and Table V, maximum depths, on the average, are attained late in the summer. It is obvious that burrows are deepened during the summer. It is possible, however, there is differential survival of colonies that have made deeper nests, for as the soil dries during the summer, it may happen that only

deep nests reach levels where the soil is damp enough. If this is true, selection would probably favor colonies using nests of the previous year established by more than one queen. The enormous mortality of colonies noted in a preceding section was so far as known mostly in nests started by single queens. Colonies started each spring by several queens may occupy the same burrows for several years in succession and perhaps deepen the burrows somewhat each year. The lower parts become filled with dirt (often loose) during spring and early summer, but this may be cleaned out or new branches made during the summer. The deepest burrow

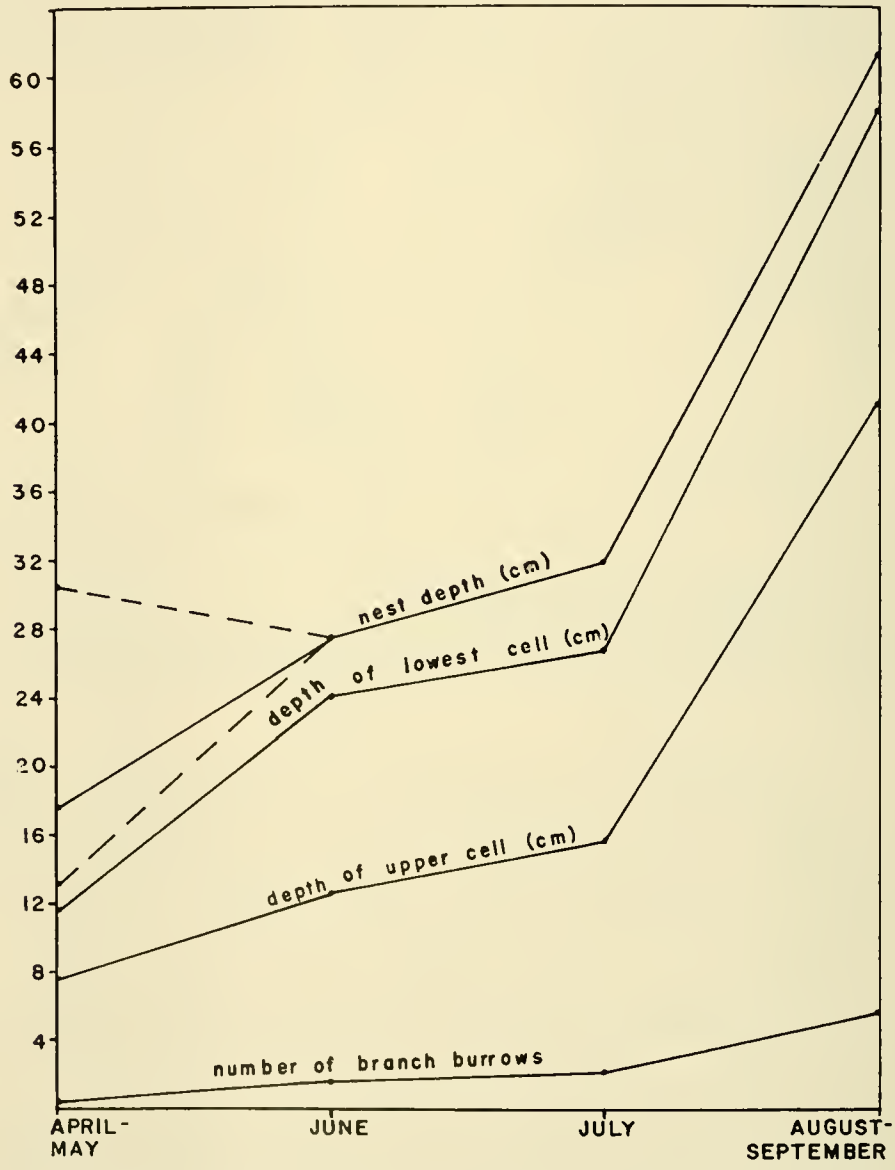


FIGURE 17. Graph showing mean nest depth, cell depths, and mean number of branch burrows. For April-May, broken lines also show depths of newly established nests and of old nests of the previous year that are being re-used. Other statistics concerning these matters appear in Table V.

found (in August) was 93 cm. deep, much branched after the manner of Figure 14. The shallowest, late summer or fall, burrow was only 14 cm. deep.

As shown in Figure 17 and Table V, the number of branch burrows is much greater in the large nests late in the season than in the small queen nests. Nonetheless the number of branches is not as well correlated with burrow depth as might be supposed. The correlation coefficient (r) of nest depth with number of branch burrows ranges from .45 to .50 during the summer months. Figure 14 shows a nest with about the maximum number of branch burrows, while Figures 13 and 16 show rather deep nests with few branches.

Of course the level of occupied cells descends with the deepening of the burrows (Figure 17 and Table V). In the queen nests in the spring the uppermost cell is quite regularly about 8 cm. below the

TABLE V.—Nest Depths (in centimeters) and Number of Branches. For total depths, statistics on new nests and on nests of the previous year are segregated in April and May. Later in the season it becomes impossible to distinguish new from old nests. n = number of nests examined; $\bar{x}$ = mean; SE = standard error of mean.

	Nest depth				Depth of upper cell			
	n	$\bar{x}$	SE	range	n	$\bar{x}$	SE	range
April-May	46	17.54	1.539	9.5–55	47	7.74	.182	3.5–11
new	35	13.50	.452	9.5–24				
old	11	30.41	4.540	17–55				
June	31	27.56	1.960	10–52	30	12.50	.951	6.5–30
July	24	32.06	2.170	18–67	23	15.50	.951	9–27
August-September	26	61.23	4.656	14–93	21	41.02	4.515	7–63

	Depth of lower cell				Number of branches			
	n	$\bar{x}$	SE	range	n	$\bar{x}$	SE	range
April-May	27	11.72	.455	7–18	29	.48	.162	0–3
June	30	24.20	1.790	9–48	30	1.60	.568	0–11
July	22	26.82	2.188	13–55	24	2.21	.528	0–12
August-September	21	57.95	4.65	9–84	24	5.75	1.029	0–16

surface of the soil, although depths ranging from 3.5 to 11 cm. have been recorded. After workers mature and the burrows are deepened, new cells are constructed at deeper and deeper levels and at increasingly variable levels, as shown in Table V. Cells from which bees have emerged are filled with dirt, usually very soon after emergence, so that the number of used cells that have not been filled with earth in any one nest is always very small except occasionally when the adult population is for some reason much reduced.

The cells themselves are subhorizontal, sloping downward slightly to their posterior ends, bilaterally symmetrical, the lower surface being flatter than the others, very smooth on the inner surfaces which are lined with a thin coating of waxlike material (Figure 42). Measurements of cells range from 5 to 6.6 mm. in length and from 2.8 to 3.2 mm. in diameter. The variation in length is partly due to variation in the exceedingly short lateral burrows connecting cells to the main burrows. The laterals may be said to be so short as to be absent. Ordinarily after an egg is laid in a cell, it is closed by means of a plug of loose, friable soil. Sometimes when plaster of Paris is poured into a nest, it enters a few of the cells. We do not know if such cells were really open; perhaps the plaster merely pushed aside the delicate plugs. It is clear that plugs are normally present; it is also clear that plugs are absent or destroyed with equal frequency in cells of all ages, including those containing pupae. It is therefore most unlikely that there is any progressive feeding of larvae, since if that were the case one would expect to find plugs more frequently absent in cells containing larvae of certain ages. Occasionally a nest was found in which plaster entered nearly every cell. It should be remembered that in *L. malachurum* (Kirby) and other species in Europe some authors have insisted that the cells are open while others have found them closed. Perhaps there is variability in the strength of the plugs or even in their presence. Sakagami and Michener (in press) have discussed the various statements in the literature concerning this matter. As shown in the figures, the cells are often grouped more or less close together, but do not form distinct clusters as in some other halictine bees. (See discussion of halictine architecture by Sakagami and Michener, in press).

The numbers of cells in queen nests that had probably reached the age where no additional cells would be made until emergence of workers are shown in Figure 18. It is evident that nests made by a single queen usually contain about five cells, although there is

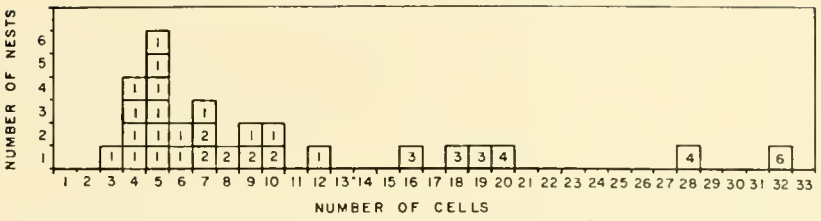


FIGURE 18. Histogram showing numbers of cells in queen nests. Queen nests containing only eggs and young larvae, or which for any other reason seemed to be still growing, were excluded from consideration. Exceptions are nests containing 28 and 32 cells which were included because of the large numbers of cells (and queens) even though they might have produced even more cells. The numbers in the squares indicate the number of queens found in each nest. It seems probable that two queens were in nests having 10 and 12 cells, but that one disappeared or was lost in two cases.

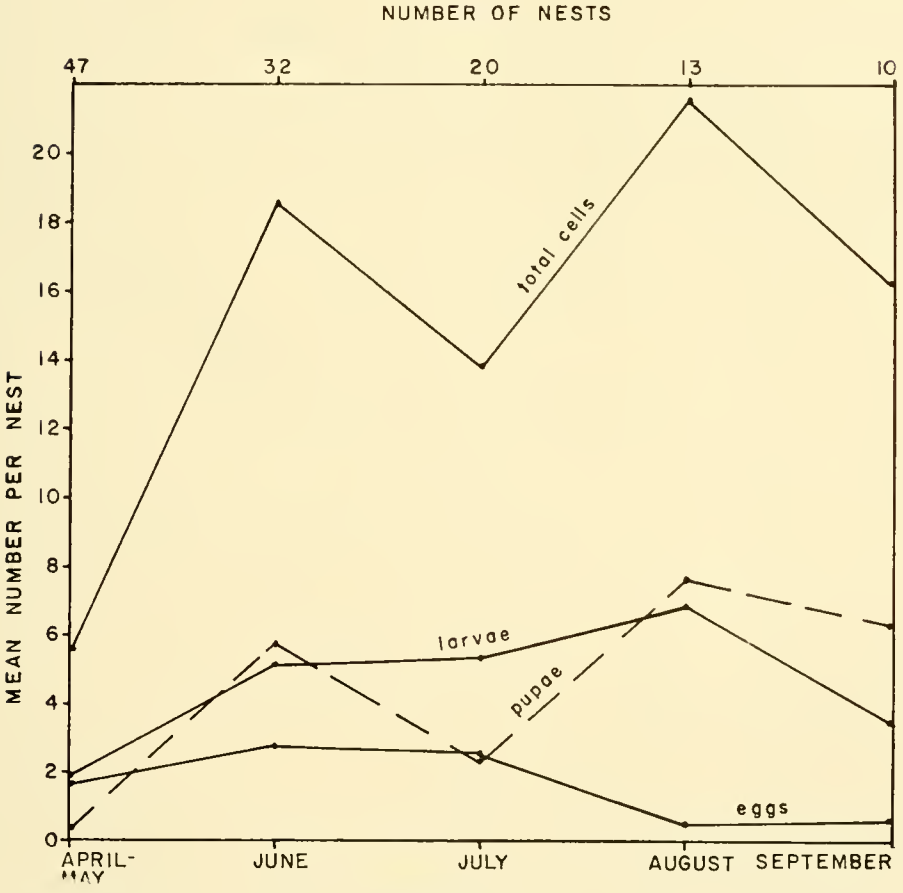


FIGURE 19. Cells and their contents. The excess of the total cells over eggs + larvae + pupae is due to cells under construction and being provisioned as well as old abandoned cells that were not filled with earth. The dip in cell number in July compared to June and August may be a result of small sample sizes or baised sampling resulting from comparing in this figure data obtained in different nesting places and in different years; or it may represent biological fact. However, the only year (1952) for which we have good records for both June and July from the same nesting area suggests that the dip in July did not occur in that place in that year of relatively moist soil [June $\bar{x} = 12.3$ ($n = 22$); July $\bar{x} = 15.6$ ($n = 12$)].

considerable variation. Nests occupied by more than one queen contained correspondingly more cells. The average number of cells per nest was 10.1 (This mean is higher than shown in Figure 19 and Table VI because incomplete nests are included in the latter figure and table).

After emergence of the workers, the number of cells increases, as shown in Figure 19 and Table VI. The maximum number found in any one nest was 90 (Figure 14), found near the end of June, but nests with over 50 cells were found at various times until early September. During each of the summer months nests with only 4 to 7 cells were also found, and even two or three nests without cells. The nests without cells were not new ones, but old ones with earth-filled remnants of cells, but without new ones. The above figures for cell numbers, and those used in preparing Figure 19 and Table VI, exclude old, used cells filled with earth and in-

TABLE VI.—Number of Cells and of Eggs, Larvae and Pupae Per Nest. n = number of nests; $\bar{x}$ = mean; SE = standard error of mean. Under the heading "%" are shown the percentage of the cells that contain eggs, larvae, and pupae.

	n	Number of cells			Number of eggs			
		$\bar{x}$	SE	range	$\bar{x}$	SE	%	range
April-May	47	5.45	.867	0–28	1.81	.574	33.2	0–24
June	32	18.56	4.025	1–90	2.78	.891	15.0	0–19
July	20	13.75	2.385	4–47	2.65	.956	19.3	0–14
August	13	21.62	5.281	0–67	.62	.331	2.8	0–4
September	10	16.30	4.690	0–52	.70	.422	4.3	0–4

	n	Number of larvae				Number of pupae			
		$\bar{x}$	SE	%	range	$\bar{x}$	SE	%	range
April-May	47	1.92	.375	35.2	0–10	.06	.064	1.1	0–3
June	32	5.19	1.493	28.0	0–34	5.84	1.327	31.5	0–34
July	20	5.40	1.125	39.3	0–21	2.45	.541	17.8	0–7
August	13	6.92	1.806	32.2	0–23	7.69	2.379	35.6	0–23
September	10	3.50	1.609	21.5	0–12	6.40	3.140	39.3	0–30

clude only those containing immature stages of bees and those in the process of being constructed or provisioned and such old empty cells as exist.

According to the system of Sakagami and Michener (in press) nests of *L. inconspicuum* are to be classified as follows: OCh^{n}B.

Nest construction: The starting of a new nest by a single queen bee was observed several times in the spring. At this season many of the overwintered queens spend much time crawling over the surface of the ground, flying short distances, alighting here and there, and crawling more, often biting at the ground with their mandibles. Not infrequently they start to dig, but usually after making a hole one or two millimeters deep, they abandon it and continue the activity which looks like searching. This can be observed most readily in areas of nest aggregations but with patience can also be seen in many other patches of bare ground. Sometimes several such bees were seen at the same time in an area where a nest was never subsequently found. Occasionally, perhaps most commonly in the afternoons, such a bee continues its digging, disappearing into the soil in as little as 20 minutes if the soil is moist and easily worked. The digging is done with the mandibles; as the hole becomes deeper earth is pushed out with the posterior-dorsal surface of the abdomen and forms a tumulus which spreads irregularly all around the entrance of the burrow.

As explained previously, dirt excavated in digging new cells or extending the burrows in established nests is often put in old abandoned cells (which rarely stay open long) or in short branch burrows, rather than being carried all the way to the surface. We replaced the upper 10 to 20 cm. of certain nests with glass tubes which had cell-like evaginations blown in them. The bees never used these evaginations as cells but soon filled them with earth brought up as a result of work below the level of the glass tubes. Nonetheless tumuli appear at irregular intervals throughout the summer at the entrance of every nest containing an active colony of bees, for there is never enough space below the surface for all the dirt that is dug out by the bees.

The smooth areas around the nest entrances appear to be made by the bees which act as guards; such areas are absent at the entrances of nests inhabited by only a single bee, and guarding is not observed at such nests. A bee at the nest entrance can often be seen mouthing the smooth area with its labium, and also rubbing it with its front tarsi, which are bent mesad under the head. Special

attention is paid to the rim of the entrance hole, *i. e.*, to the inner margin of the smooth area. The postero-dorsal extremity of the abdomen is often used to shape this region, by patting motions when the soil is moist. Similar patting was sometimes observed to shape the outer margin of the smooth area, as is shown by the following notes made soon after a heavy rain. The smooth area had already been fairly well reformed, but the guard bee was still at work on it. She reversed herself inside the nest and backed out of the nest so that the whole abdomen was exposed and strongly arched so that the tip was directed downward. Supported within the entrance by the outside surfaces of the legs thrust against the walls, the bee tamped the smooth area with the apex of the abdomen, the whole abdomen being moved up and down. Small changes in position allowed the abdomen to tamp different parts of the smooth area. The parts close to the nest entrance were tamped as the bee slowly moved into the nest, and similar tamping continued inside of the nest, smoothing and making more firm the inside wall of the burrow.

It would seem that the diameter of the smooth area is a reflection of how far the bee can reach with the abdomen. Probably the size of various other structures of the nest are also related to dimensions of the bees, the entrance being of a size to admit only one bee at a time, the rest of the burrow being large enough to allow bees to pass one another readily.

When the soil surface is very dry and the smooth area completely gone due to crumbling of the soil, a little water allowed to soak into the soil about the nest entrance is sufficient to cause the guard to construct a smooth area. Sometimes two or three bees will work at and just inside the nest entrance simultaneously, patting with their abdomens to shape the entrance and its smooth area.

Because of the relatively uniformly colored soil in the areas of our study, we did not readily detect the working of the soil forming the lining of the burrow. Soil from deep in the nest lines the burrow to the surface in many halictine bees and *L. inconspicuum* is probably not an exception. At least this species has the ability to construct burrow linings of soil, for if we replaced the upper part of a nest with a glass tube slightly too large in diameter, or if we installed a glass window in the side of a burrow, the bees promptly lined the tube or window with soil, patting it into place with the dorso-apical part of the abdomen. This covering was much less

likely when the glass was covered (except at the times of our observations) to prevent light from entering the burrow.

If the constriction of the burrow at the surface of the ground was destroyed, then the bees would narrow the entrance again by bringing soil from deep in the nest and forming a lining around the entrance of the burrow.

Through the glass windows and tubes, as well as by observations of undisturbed nest entrances, it was possible to see that the bees bring dirt up from deep in the nest either by backing upward pushing the dirt with the dorsal apical part of the abdomen, or by moving upward head foremost, pushing the dirt with the face, especially the clypeus.

In queen nests occupied by single individuals, the uppermost cell is usually the first provisioned, and provisioning continues downward. The result is that as in Figure 6, there is usually a sequence in ages of the immature stages from oldest above to youngest below. This is not invariable, however, for sometimes a pupa will be found below a larva, for example. In nests occupied by several queens this order may persist, but more often does not. Thus in the upper right-hand branch of the nest shown in Figure 7, the mixture of eggs and small larvae is quite complete. Because of the progressive deepening of the burrow and of the level where new cells are made, the same sequence, from older above to younger below, occurs in most nests in summer and fall, when the colony contains workers. However, these nests are usually full of irregularities in the order of the cells, as can be seen in Figure 16 and, to a lesser extent, in several other illustrations.

Most nests in which cells are being constructed and provisioned have one or two complete cells ready to be provisioned, as indicated by the letter "E" on the diagrams of nests. This is true even of small insects, such as queen nests made by single queens in the spring. Contrary to many bees which make, provision, and seal a cell before starting to make the nest, *L. inconspicuum*, while provisioning one cell, seems to be making one or two others. This is true of most Halictinae (see Sakagami and Michener, in press).

Provisions and Immature Stages: In opening nests one occasionally finds fresh cells containing a mass of loose pollen on the floor (Figure 20, a). Sometimes a small lump has been moistened, presumably by honey, and hence forms an irregular firm mass. When the provisions are complete, however, there is virtually no dry pollen in the cell; all of it is worked into a smooth mass. This

mass of provisions has the form of a flattened sphere (Figure 20, b), 1.9 to 2.5 mm. in horizontal diameter and 1.4 to 2.0 mm. in vertical diameter. The egg is white, curved, 1.33 to 1.50 mm. long about .25 mm. thick (Figure 20, b), and is supported by its two ends on top of the mass of provisions. The larva feeds down into the upper anterior* part of the pollen mass (Figure 20, c, d, e), finally turns over with what is left of the pollen mass (Figure 20, f). After the larva has eaten all the food it lies with its head toward the anterior end of the cell. The feces are then voided as soft pellets pushed against the upper posterior portion of the cell, where they form a firm layer (Figure 20, h; Figure 43). Voiding of the feces took

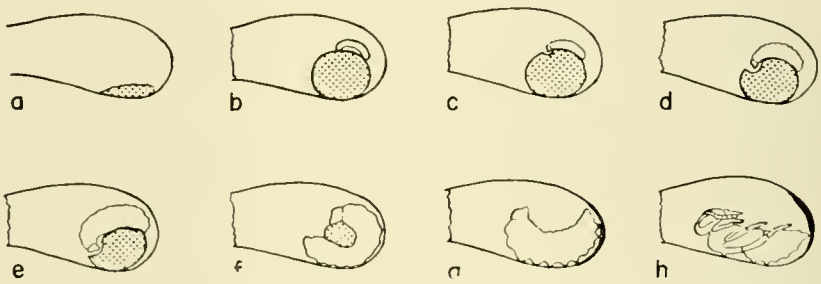


FIGURE 20. Diagrammatic saggital sections of cells of *Lasioglossum inconspicuum*. a, loose pollen placed on floor of cell; b, mass of provisions with egg on top; c, d, e, f, larva in different growing stages; g, prepupa; h, pupa.

a day and a half for specimens in the laboratory. The larva, at this stage, straightens out and becomes a prepupa, and ultimately a pupa.

We have not done much work on the duration of the developmental stages. We have found it difficult to rear the larvae in the laboratory. We were repeatedly successful in rearing prepupae through the pupal stage to adults but the younger larvae died. The data given below are based entirely on females (probably workers). The duration of the pupal stage varies enormously with temperature; probably that of the other stages varies equally. Prepupae taken on May 10 pupated on May 12; the eyes of these pupae were black 10 days later and adults emerged after another 8 to 9 days; thus the entire pupal stage at room temperatures of 70° to 75° F. required 18 or 19 days. By contrast, another group of prepupae pupated on June 12, and developed at a time when the room temperature in which they were kept ranged from 90° to 95° F. These pupae had black eyes three days after pupation and adults emerged

* Here and elsewhere the words anterior and posterior are applied to cells and structures therein with reference to the orientation of the egg. Probably in all bee cells the anterior end of the egg is toward the oriface of the cell, *i. e.*, toward plug that is made from the outside by the mother bee as she closes the cell.

three days later, so that the total pupal stage required only six days, or about one third of the time required by the group mentioned previously. Obviously the rate of development will vary widely according to weather and the depth of the cells. When pupae were reared at temperatures of 81°-83° F., this stage required eight or nine days; this is probably a reasonable estimate of the duration of the pupal stage in summer.

Among 70 nests fully excavated during June, July, and August, we found totals of 159 eggs, 354 larvae (including prepupae), 324 pupae and 31 teneral adults with milky wings, still in their natal cells. By omitting vernal and autumnal nests from this tabulation, we have avoided the spring nests that have not yet had time to produce pupae and the autumn nests that lack eggs and young larvae while containing many pupae. The total numbers of individuals of the various stages given above ought to be proportional to the duration of the stages. If this be so, the egg stage is a little less than half as long as the pupal stage or perhaps four days, the larval stage is perhaps slightly longer than the pupal stage, say nine days, and the teneral adult remains in its cell for a period less than one tenth as long as the pupal stage, that is somewhat less than one day. This would give us a total of about 21 days from egg laying until emergence of the adult from its cell under summer conditions.

The interval between the average date when pollen collecting was first seen in the spring and the average first date when workers were seen at the nest entrance is 43 days. This period must be roughly comparable to the egg laying to emergence period discussed in the preceding paragraph although pollen is collected and a cell provisioned before the egg is laid; the 43-day period is about twice the estimated summer developmental period of 21 days. This corresponds nicely to the observed duration of the pupal stage in May (18 or 19 days), which was about twice the observed duration of this stage at 80° to 83° F. (8 or 9 days). As indicated in a later section on "Behavior of Queens," observations of individual nests in the field suggest an egg-laying to adult period of about 30 days in the late spring.

INDIVIDUAL AND SOCIAL BEHAVIOR

Aggregations of Nests: As stated previously under "Distribution of Nests," many of the nests are isolated. On the other hand, many are in loose aggregations. Nests were found in relatively few of the apparently suitable areas and aggregations in even fewer.

Usually nesting aggregations do not occupy all of the apparently suitable areas of soil in which they occur. It is not clear why the aggregations occur, in view of the apparent success of isolated nests elsewhere and the abundance of seemingly suitable soil. The areas of concentration are not necessarily areas of successful nesting; we have seen whole aggregations disappear, probably due to death of bees. The same sites are often attractive spring after spring, and many queens establish nests in areas of nest aggregations, even though few nests may have survived the summer in those places. Possibly the odor of nests or bees attracts others to the same vicinity; perhaps a factor contributing to development of aggregations is a tendency of the young queens to return to the vicinity of birth to make new nests.

Nest Populations: The number of adult female bees in one colony (*i. e.*, one nest) varies from one to 25. Most queen nests in the

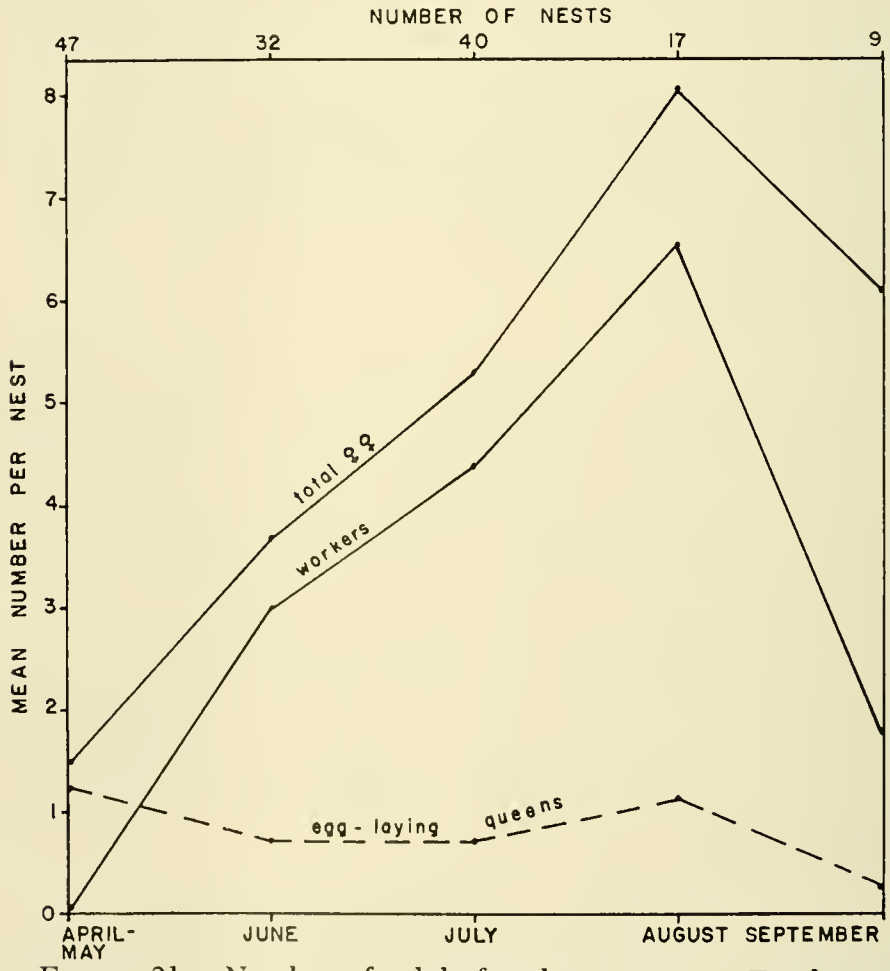


FIGURE 21. Number of adult females per nest. Egg-laying queens (groups A and B) were recognized by dissection. The excess of the total over workers (groups C and E) plus queens is due to individuals that were doubtful as to caste as well as, particularly in September, to young queens (group D). The meaning of the lettered groups is explained later in the text.

spring contain only a lone queen, although we have studied nests at that season inhabited by as many as six queens (Figure 18). With the production of workers, the population of adults in the nest rises, reaching a peak in August (Figure 21, Table VII) of over eight females per nest, on the average. This average total, of course, includes numerous small colonies, for throughout the season many colonies die out, and during the process they often reach the stage of having only one or two bees each.

TABLE VII.—Number of Adult Females Per Nest. n = number of nests; $\bar{x}$ = mean; SE = standard error of mean. Queens were fertilized egg-laying individuals; workers were usually unfertilized and had not over one or two enlarged oocytes; other females were doubtful as to caste or were young queens. The meaning of groups A, B, C, D, and E, is explained in the text later. The number of nests shown here is more than indicated in Table VI and related materials because of nests whose populations were preserved but for which data on cells, etc., was not recorded.

	n	Queens (groups A and B)			Workers (groups C and E)			Other females (group D and ungrouped)		
		$\bar{x}$	SE	range	$\bar{x}$	SE	range	$\bar{x}$	SE	range
April-May..	47	1.21	.161	0–6	.09	.053	0–2	.19	.072	0–2
June....	32	.72	.138	0–3	3.00	.803	0–16	0		
July....	40	.70	.090	0–2	4.48	.475	0–14	.18	.062	0–2
August..	17	1.18	.182	0–3	6.65	1.654	0–22	.24	.106	0–1
September...	9	.22	.147	0–1	1.78	.782	0–6	4.11	1.505	0–15

Males: The occurrence of males during the season is indicated in the section on the seasonal cycle. Males leave their nests soon after emerging from their cells; therefore the few males found in the nests do not give a correct idea of the proportion of males produced. Figure 22 shows the percentages of the young produced at various seasons that are males. In contrast to *L. rhytidophorum*, (see Michener and Lange, 1958) there is no clear peak of male production in spring. Instead, in May and early June no males seem ordinarily to be produced. Males have been recorded, as indicated in the section on the "Seasonal Cycle," as early as June 1 (two different years) and June 10. Unfortunately these early males have not been preserved and it is now apparent that they might

FIGURE 22. Graph showing percentage of pupae and of young adults (in closed cells) that are males. Each month is represented by two points, one for the first half, one for the second half. The number of pupae and young adults examined during each period is shown at the top of the graph.

have belonged to *Lasioglossum* (*Paralictus*) *cephalotes*, a parasite in the nests of *L. inconspicuum*.

Most of the males indicated in Figure 22 were produced in nests which were also producing females. However, two nests were found which were producing only males. On July 15, 1951, a nest was opened containing five male pupae but no eggs nor larvae. The nest had been marked on June 6, at which time it contained at least two foraging workers. By July 15 it has been long closed by rains and was unrecognizable at the surface of the ground. It seems possible that the founding queen died, that her unfertilized workers laid at least five eggs, and that after the workers died these males continued their development.

The other nest which produced only males was opened on June 21, 1952. It contained seven male pupae as well as three larvae of unknown sex and three adult females. Two of the latter were workers, both with very slender ovaries while one was a queen; unfortunately her spermatheca was lost and we do not know if she was mated or not. However, she was probably the mother of the

workers. She contained no very large oocytes (longest .91 mm.), not a surprising finding since the nest contained no eggs or small larvae. The reason for this nest producing males at this season is unknown.

Males visit flowers for nectar but are most often seen flying about the nesting areas. At a nesting area like that at Potter's Lake where the vegetation (except for large trees) is very low, the males zig zag over the soil or small plants, usually flying from two to 12 cm. above the ground. Where there is higher vegetation, they fly higher, often flying in numbers around the weeds at altitudes as high as one meter. In Riverside, California, where *L. inconspicuum* has be introduced, around the home of Mr. P. H. Timberlake, males were noted in immense numbers flying rapidly about small trees in the nesting area; although there were more at heights of one or two meters, some could be seen around foliage five meters above the ground.

When males are scarce, individuals often make these flights alone but when they are numerous they usually dance in loose groups, each individual zigzagging with great rapidity. Often one or a few will alight on the ground or foliage over which they are flying, only to resume flight in a few seconds or minutes. Flights such as this, in the vicinity of nests, are usually in the sun when the temperature is moderate but in the middle of the day on hot days, when the temperature in the shade rises above about 100° F., the flights move into partially shaded areas. At open nesting sites where there is no shade from weeds or nearby trees, the flights cease and the males disappear during the warmest hours of hot days.

We are not sure whether we have observed mating or not. Males, sometimes two to four of them simultaneously, often pounce on females. Usually they are repulsed immediately, often only after rolling over on the ground, but sometimes contact lasts for about 10 seconds; this may be copulation. Males pounce upon any halictine of about the right size. Young females and old senile females that fly about the nesting area unable to find their nests are most commonly pounced upon by males, but foragers at nearby flowers, males of other species of *Chloralictus*, and females of the parasite, *L. (Paralictus) cephalotes*, are all often attacked. Since such activity has been noted on the ground, on foliage, and on flowers; we assume that mating may occur at any of these places. We believe that it usually occurs near the nesting site rather than on distant foliage or flowers.

It is significant that males collected on flowers varied in mean size according to the season. It has been shown elsewhere (Michener and Lange, 1958, 1959) that wing length, face width, and other body measurements in halictine bees are highly and positively correlated so that any one can serve as a fair index of size. Facial width and wing length were measured for series of specimens collected in different months as shown in Figure 23. For both measurements the mean for July males was below means for June and September (difference significant at the 5% level; Q test, Snedecor, 1956, p. 251); differences between the June and September means were not significant. Only small numbers of specimens were available for August; they were intermediate in mean size between the July and September series. As will be shown later, the seasonal

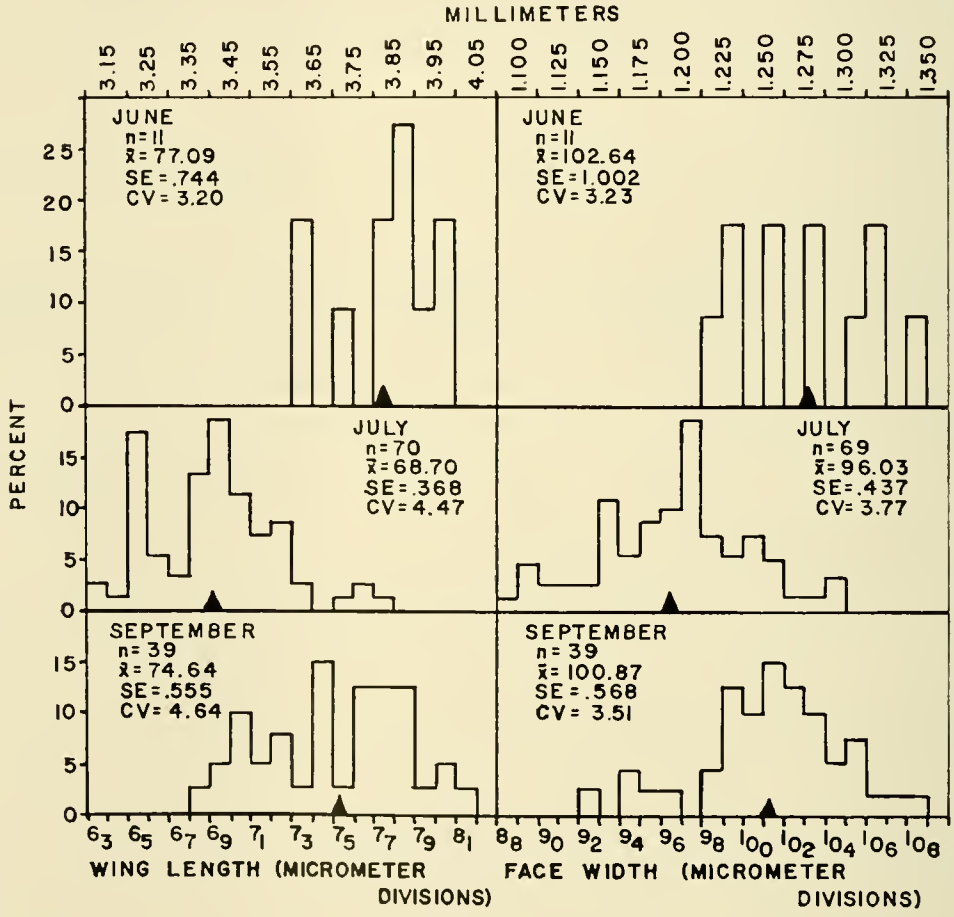


FIGURE 23. Histograms showing wing lengths (left) and head widths (right) of males of *Lasioglossum inconspicuum* collected on flowers in the months of June, July, and September. Statistics are shown in micrometer divisions with equivalents in millimeters across the top. The means are marked by black triangles at the bases of the histograms. Abbreviations; n = number of individuals measured, $\bar{x}$ = mean, SE = standard error of mean, CV = coefficient of variation.

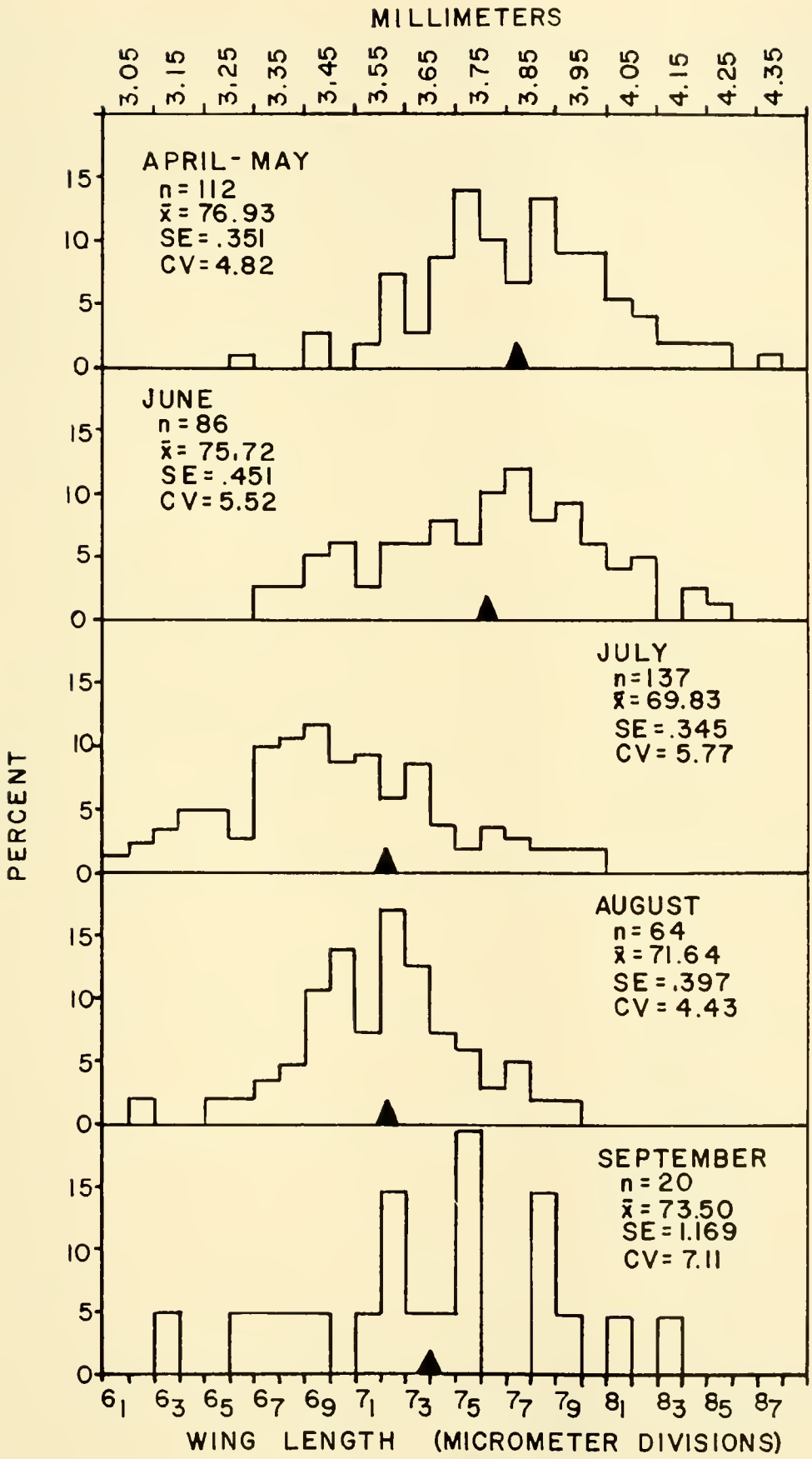
size variation of the males is positively correlated with that of females.

Variation in Size Among Field-collected Females: Females, like males, collected on flowers varied in mean size according to the season, as shown in Figures 24 and 25. Minimum size occurred in July as determined by wing length, in August as judged by head width. To judge by observations of nests, the April and May individuals should all be queens, the June, July and August individuals should nearly all be workers, while those taken in September should be a mixture of workers and young queens. The relatively low means for September (as compared to April and May), and the high coefficients of variation for that month, must be due in part to the mixture of workers and young overwintering queens on the flowers during that month. The young queens that actually overwinter are the same individuals that visit flowers in April and May and should, of course, be of the same size unless there is differential mortality of smaller individuals.

The means shown in Figure 24 are significantly different at the 5 percent level (a posteriori Q tests among means, Table 29, upper 5 percent, Pearson and Hartley, 1956) except that September is not significantly different from June and August, and June is not significantly different from April and May. The means shown in Figure 25 are significantly different at the 5 percent level by the same method except that July and August are not significantly different from one another or from September, and June is not significantly different from April and May.

Caste Differences: The interpretation suggested in preceding sections indicates the presence of more or less different female castes (queen, worker). In order to study the castes, entire populations from over 150 nests were captured and dissected. Occasionally a bee escaped, but insofar as possible complete nest populations were obtained (1) by excavating in cool cloudy weather when no bees were afield; or (2) by plugging nests that were to be opened either at night or during other hours when all the bees were presumably in the nest; or (3) by watching a nest for one and one half hours or more before excavating it, in order to capture returning bees, meanwhile preventing the departure of all individuals from the nest. All individuals from such nests were dissected to determine ovarian development, presence of pollen in the crop, and of sperm cells in the spermatheca.

FIGURE 24. Histograms showing wing lengths of females of *Lasioglossum inconspicuum* collected on flowers in various months. Statistics are shown in micrometer divisions with equivalents in millimeters across the top. The means are marked by black triangles at the bases of the histograms. These measurements cannot be compared directly with wing measurements in subsequent tables for the wings were measured by a different person and in a different manner. Abbreviations: n = number of individuals measured, $\bar{x}$ = mean, SE = standard error of mean, cv = coefficient of variation.


MILLIMETERS
3.05
3.15
3.25
3.35
3.45
3.55
3.65
3.75
3.85
3.95
4.05
4.15
4.25
4.35
APRIL - MAY
n = 112
x̄ = 76.93
SE = .351
CV = 4.82
JUNE
n = 86
x̄ = 75.72
SE = .451
CV = 5.52
JULY
n = 137
x̄ = 69.83
SE = .345
CV = 5.77
AUGUST
n = 64
x̄ = 71.64
SE = .397
CV = 4.43
SEPTEMBER
n = 20
x̄ = 73.50
SE = 1.169
CV = 7.11
PERCENT
0
5
10
15
61 63 65 67 69 71 73 75 77 79 81 83 85 87
WING LENGTH (MICROMETER DIVISIONS)

On the basis of ovarian development and presence or absence of sperm cells in the spermatheca, females can be divided into several groups as follows:

A—Fertilized, with ovaries much swollen, usually to the point that enlargement of the posterior portions of one or both ovaries often forces the anterior portions of one or both into sharp bends or convolutions (Figure 26). Such ovaries seemed more swollen than in the corresponding class of *L. opacum* and *rhytidophorum* (Michener and Lange, 1958), as would be expected since the first is a nonsocial species and the second has shorter-lived queens than those of *inconspicuum*. No doubt *inconspicuum* queens produce more eggs than those of either of the aforementioned species of *Chloralictus*. The ovaries of none of these species are nearly as large, however, as those of the species with perennial nests and large colonies (Plateaux-Quénu, 1959).

B—Fertilized, with ovaries swollen but not so much as in Group A, not sharply bent, usually one or two ovarioles in each ovary not swollen (Figure 27).

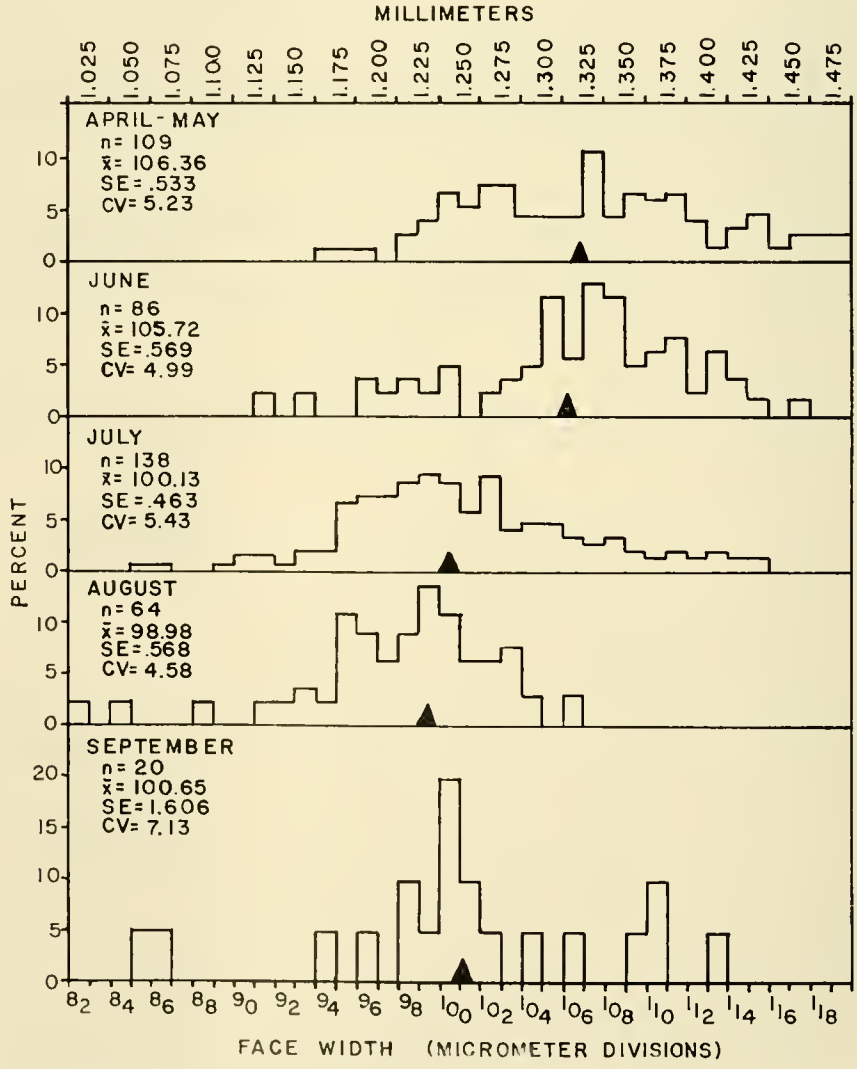
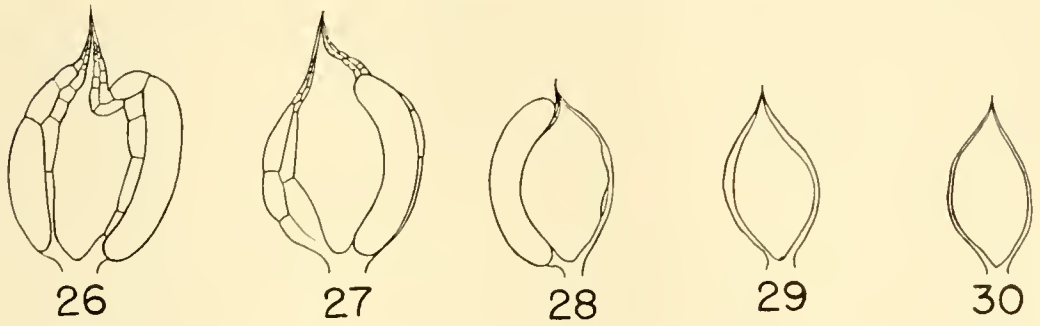


FIGURE 25. Histograms showing head widths of females collected on flowers in various months.

C—Unfertilized, with ovaries slender except for one enlarged oocyte in one ovary, or rarely one in each (Figure 28).

D—Fertilized, with slender ovaries.

E—Unfertilized, with slender ovaries. Because so many bees fell in this group, it was decided to divide it into two arbitrary subgroups for separate analysis. These were E′ with very slender ovaries (Figure 30) and E″ with merely slender ovaries (Figure 29).



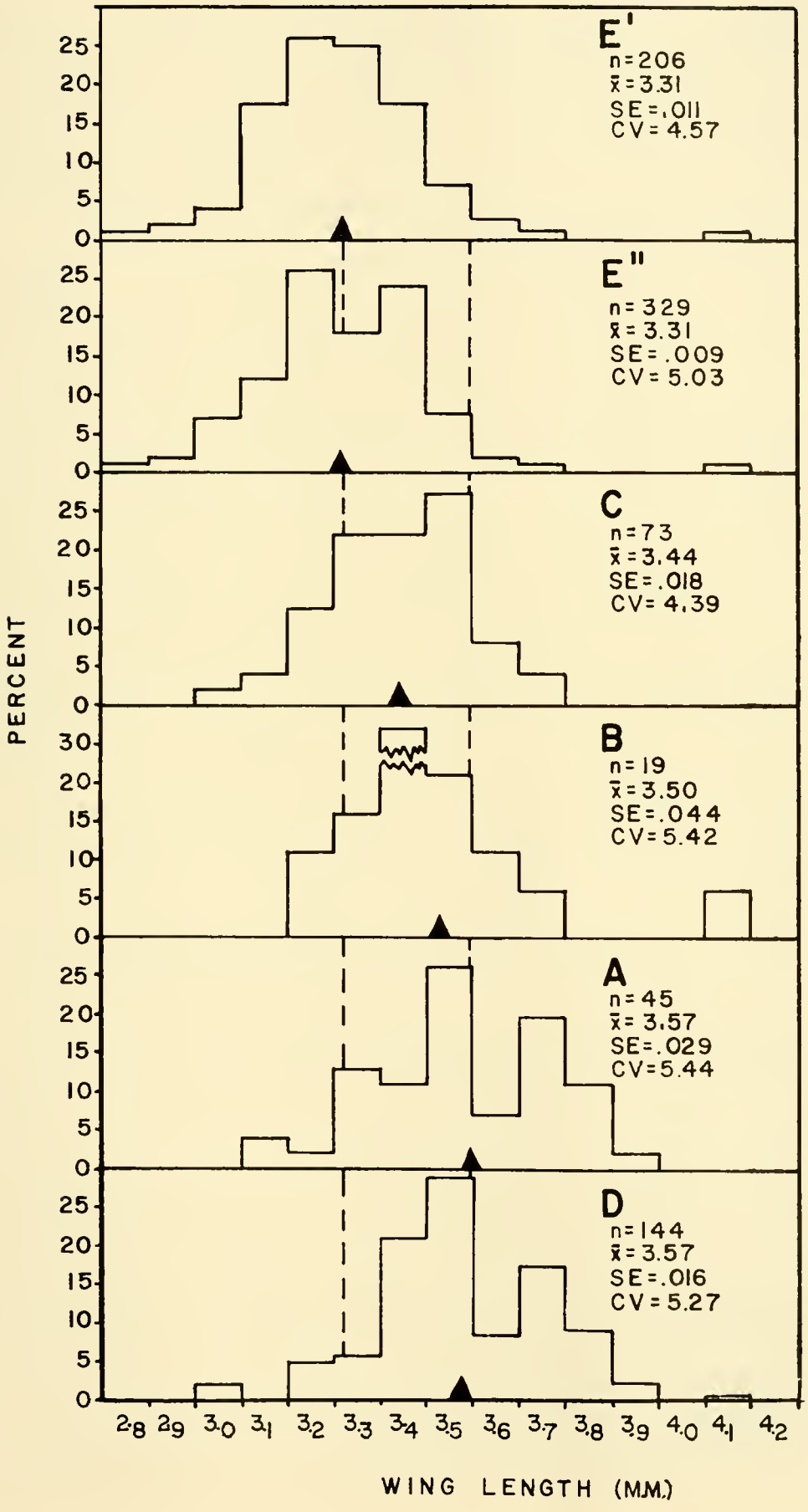
FIGURES 26 to 30. Ovaries. 26, group A (queen); 27, group B (queen); 28, group C (worker); 29, Group E″ (worker); 30, group E′ (worker).

From the standpoint of ovarian size, the groups merge. All females emerge from their pupae as Group E′. Some remain in that condition while others develop into one or another of the other groups. It is therefore to be expected that intermediates would occur. There is also excellent evidence that ovarian size may be reduced, so that progress from A to B may occur but probably not as far as D. If a group C female lays an egg she would revert to group E. Peculiarly-shaped ovaries with irregular swellings or with a developing oocyte that is much shorter than normal occur occasionally. Such individuals were placed rather arbitrarily in the classification indicated above.

In a certain percentage of individuals dissected the spermatheca was missed, or lost before it could be examined for the presence of sperm cells. In some cases such specimens were included in the analyses which follow. For example, since virtually every individual taken in April and May is fertilized, such specimens were included in group A or B even if proof of fertilization was not obtained.

Figure 31 shows the sizes (wing lengths) of females segregated into the groups listed above. In view of the seasonal cycle of the species and the differentiation of castes explained below, and to make the groupings more biologically significant, group D is limited for purposes of Figure 31 and related discussion to individuals obtained from October to May (overwintering or overwintered queens) while the other groups are limited to individuals taken in June, July, or August. In this species there are very few fertilized

FIGURE 31. Histograms showing wing lengths in millimeters of females belonging to groups A to E. These are groups based on ovarian development and presence or absence of sperm cells in the spermatheca, as indicated in the text. The histogram for group D is based on specimens taken from October to May; the other histograms are based on specimens taken from June through August. Means are shown by triangles on the base lines. The vertical broken lines are only to facilitate comparison and represent the minimum mean (group E′) and the maximum mean (group A).


E'
n=206
x̄=3.31
SE=.011
CV=4.57
E"
n=329
x̄=3.31
SE=.009
CV=5.03
C
n=73
x̄=3.44
SE=.018
CV=4.39
B
n=19
x̄=3.50
SE=.044
CV=5.42
A
n=45
x̄=3.57
SE=.029
CV=5.44
D
n=144
x̄=3.57
SE=.016
CV=5.27
PERCENT
2.8 2.9 3.0 3.1 3.2 3.3 3.4 3.5 3.6 3.7 3.8 3.9 4.0 4.1 4.2
WING LENGTH (MM.)

workers; therefore there is no large number of group D individuals in summer, as in *L. rhytidophorum.*

It is apparent that, correlated with the functional differences responsible for segregation of individuals into groups A to E, there exist certain size differences, as indicated by measurements of wing lengths. There are not, however, external morphological differences between the female castes as in bees like *Trigona* and *Apis.*

No difference in size exists between groups E′ and E″. These constitute the typical workers. Group C consists of workers which may lay one or more eggs. Their mean size is larger than that of workers with slender ovaries. The difference is significant at the one percent level (Q test, a posteriori, among means, Table 29, upper one percent, Pearson and Hartley, 1956). The remaining groups consist of queens. Group D, consisting almost entirely of overwintering females, should represent queens as a whole; its mean size (as measured by wing length) is significantly different from that of group C at the one percent level. During the active season queens are divided into two groups, A and B, according to ovarian size. Those falling in group A have a mean wing length slightly but not significantly larger than those falling in Group B. The mean wing length of groups A and B are not significantly different at the 5 percent level (Q test, a posteriori, among means, Table 29, upper 5 percent, Pearson and Hartley, 1956) from that of group D. The mean wing length of group B is not, but that of group A is significantly different from that of group C at the 5 percent level.

Since queens average larger than workers, one might suspect that in any one nest the queen would be larger than the workers which must usually be daughters of the queen. While this is more often true than not, nests were commonly found in which one or more of the workers was larger than the queen or queens. In June 77.7 percent of the nests studied had the queen (or at least one of the queens in nests containing more than one) larger than any of the workers. In July and August comparable figures were 65.2 percent and 58.3 percent, respectively. That the queens average larger in June than in July and August, probably because of replacement of some or many overwintered individuals, is suggested in the section on "Seasonal Differences in Size," and would explain the progressive reduction in the percentages shown above.

There is no correlation between worker size and colony size in this species.

It is noteworthy that in this species the smallest workers are

smaller than the smallest queens. This is not true of *L. rhytidophorum* in which the entire range of size variation of the workers overlaps that of the queens, although the largest queens are larger than the largest workers (see Michener and Lange, 1958). Thus it seems that the differentiation of the castes from the standpoint of size is more complete in *inconspicuum* than in *rhytidophorum*, a conclusion that is not surprising in view of the greater differentiation of the castes from the viewpoints of longevity and ovarian development. That there is no necessary correlation among various kinds of caste differences is shown, however, by Plateaux-Quénu's (1959) study of *Lasioglossum marginatum*, a species with queens and workers well differentiated in behavior, longevity, etc., but equal in size. Unfortunately suitable statistical data are not available for such well-studied species as *L. malachurum*.

Seasonal Differences in Size: It is evident that part of the seasonal variation in size shown in specimens caught on flowers (Figures 24 and 25) is due to the caste differences correlated with ovarian size and mating. Overwintering individuals are all queens (group D). In April and May they are the bees making and provisioning new nests. In the fall new overwintering individuals are produced. In the months of June through August, most of the individuals on flowers are workers (groups C and E). It is therefore not surprising that spring and fall individuals taken on flowers are larger than those taken during the summer. However, during the summer months differences were also noted among the monthly mean wing lengths of field caught specimens and some of the monthly means were significantly different from others.

In order to elucidate such variation during the summer, seasonal size variation of bees removed from nests and segregated as to group was investigated. The results are shown in Table XIII. Group B is excluded since it is represented by so few individuals; group D does not appear in the table since virtually all bees of that group (all those utilized in Figure 31) were overwintering or overwintered queens. It is evident from Table XIII that the June individuals average larger, July and August ones smaller. This fact is particularly noteworthy among queens (group A), where the August individuals average larger than those taken in July, and among workers with one or two large oocytes (group C), where the August individuals average smaller than those taken in July. The differences between monthly means for group C are statistically significant at the one percent level and the difference

between June and July means for group E are significant at the five percent level. The consistently larger size in all lettered groups for June than for July and August, considered with like fluctuations in field caught females (Figures 24 and 25) and males (Figure 23), makes reasonably clear that June individuals of each lettered group do average larger than those taken in July and August.

The mean sizes of individuals with unworn mandibles (presumably young adults) (last column, Table VIII) practically do not vary from month to month. Presumably most of these individuals would become group E workers. Note the similarity of

TABLE VIII.—Wing Length (mean and their standard errors) of Females Belonging to Various Groups (explained in text). Not all were taken from nests. Comparable data on unworn and presumably young individuals obtained from nests during the summer months are given in the last column. The numbers of individuals examined are shown in parentheses.

	E	C	A	Unworn
June.....	3.36 ± .028(60)	3.56 ± .033(15)	3.65 ± .051(15)	3.31 ± .045(28)
July.....	3.30 ± .010(265)	3.45 ± .029(23)	3.50 ± .045(18)	3.29 ± .016(105)
August...	3.31 ± .010(210)	3.39 ± .024(35)	3.58 ± .051(12)	3.30 ± .018(59)

their mean wing lengths to those of group E workers shown in Figure 31. There is evidence presented below (section on "Behavior of Workers") showing that such workers are short lived; it is therefore not surprising, since they not only constitute the bulk of the population but also must constantly be replaced, that the bulk of the summer production is of such workers. Evidence presented below shows that queens and perhaps workers with one or two enlarged oocytes (group C) live longer than group E workers. To appear in summer collections from nests, therefore, such individuals would not need to be produced in very large numbers. The group C workers (plus perhaps various potential group C individuals, as well as group C workers that have just laid an egg and hence look like group E, and intergrades between groups C and E) visit flowers, although queens rarely do so in summer. It seems likely that the monthly fluctuation in mean size of field caught individuals results largely from such workers with reproductive tendencies, which, together with the queens, seem to average distinctly larger in June than in July or August if Table VIII is meaningful.

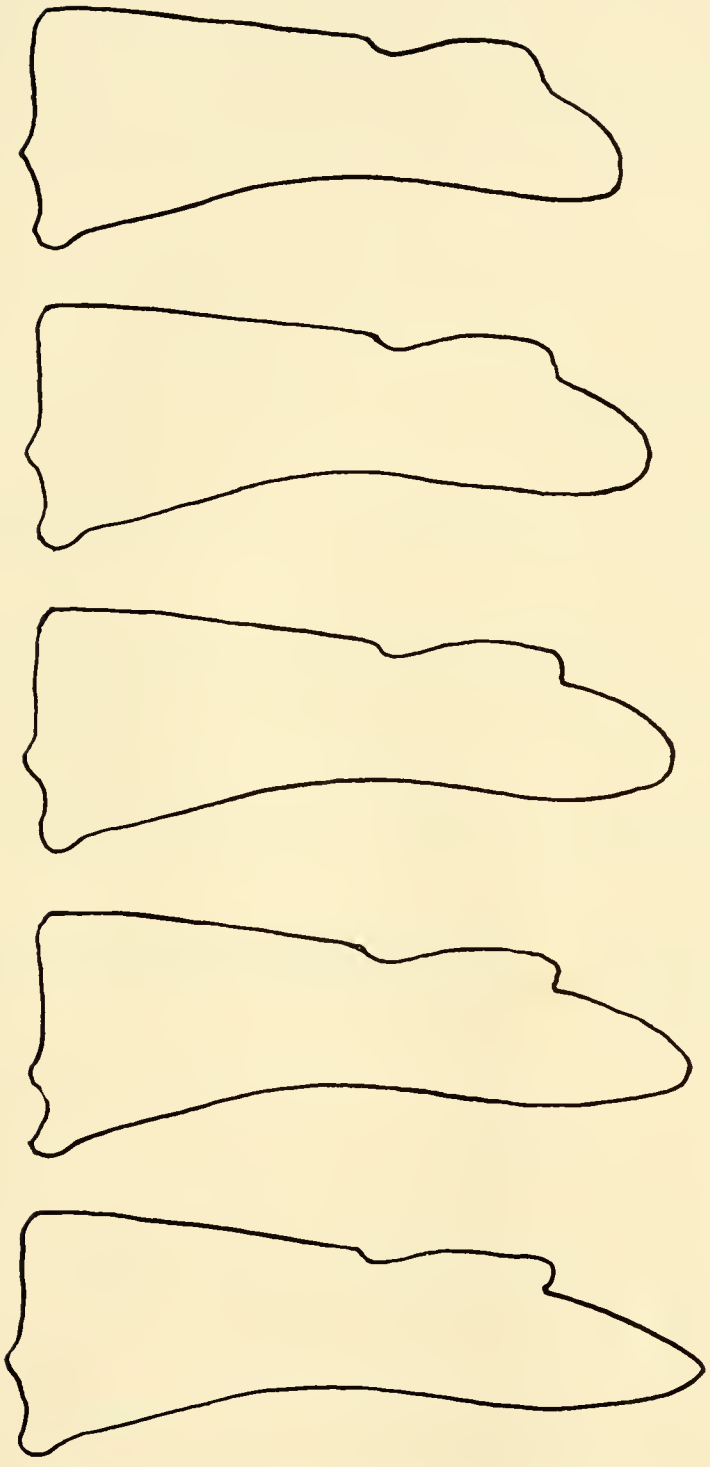


FIGURE 32. Mandibles of females showing typical examples of the five degrees of wear utilized in the analysis of activity. The indices of wear used are 1, unworn (below); 2, slightly worn; 3, well worn; 4, much worn; 5, very much worn (above).

The large size of the June queens (group A, Table VIII) compared to the overwintering queens (group D, Figure 31) may indicate differential survival of the largest queens. The smaller mean size of the July and August queens (Table VIII) may indicate that replacement queens of average size for queens (group D, Figure 31) have been produced in at least some of the nests during the summer.

Queens: The percentage of females belonging to each group at various seasons of the year is shown in Table IX. This table is based entirely on material from excavated nests. It is apparent that overwintering occurs almost entirely as fertilized females (queens) with slender ovaries (group D). The only exceptions found to this statement were three unfertilized individuals (group C) that must have overwintered and were found in different nests in April, 1955.

Because the wings are rarely nicked in this tiny species, the index of wear, unlike that used for other halictines in previous publications, is based entirely on the mandibles (1, unworn; 2, slightly worn; 3, well worn; 4, much worn; 5, very much worn; see Figure 32). The index of wear therefore reflects the amount of digging in the ground done by the bees. As shown in Table X, the overwintering bees are unworn or nearly so.

TABLE IX.—Percentages of Females Belonging to Groups A to E During Various Months. All specimens were taken from nests (data for April were obtained in the last half of the month).

	Number of bees	Percent in each group				
		A	B	D	C	E
April	35	42.9	37.1	11.4	8.6	.....
May	45	42.2	33.3	17.8	.....	6.7
June	103	18.5	3.9	.....	12.6	65.1
July	213	9.0	4.7	1.4	5.7	79.7
August	131	9.2	6.1	3.8	6.1	74.8
September	59	1.7	1.7	57.6	1.7	37.3
October	17	.....	.....	100.0	.....	.....
November–December	14	.....	.....	100.0	.....	.....

By the second half of April, 80 percent of the individuals obtained had enlarged ovaries (groups A and B) as shown in Table IX. The time of emergence from overwintering quarters appears to be highly variable, for we have seen new nests established from early April to mid-May. Nests seen and excavated by us were nearly all open ones; we would have missed any closed ones still containing hibernating bees. Therefore it is probable that less than 80 percent of the total female population develops enlarged ovaries by the second half of April. This belief is supported by the relatively high percentage of bees still having slender ovaries in May (group D, Table IX) and by the not or little worn mandibles of many bees in May (Table X).

The sharp reduction in the percentage of queens (groups A and B) in the population in June and subsequent months (Table IX) is due to the large worker populations (groups C and E). The number of queens per nest decreases only slightly and gradually through the summer months, as shown in Table VII and Figure 21, which are based for the most part on data from the same nests as Tables IX and X.

Table X shows that the average indices of wear for queens during the summer are high, probably in group A progressively higher as the summer months pass. Table XI, giving the raw data for group A and B queens lumped together, shows this trend more clearly. This trend seems to indicate that some of the overwintered queens live through much of the summer. It was our impression as specimens were dissected that at least through June and probably well into July and perhaps August, the queens that we found were mostly overwintered individuals. Survival of queens through most of the summer would also be expected since most males appear in late summer and fall, they mate with young queens that will overwinter. If replacement of the queens in nests were a general or universal event, for example in midsummer, males would be expected to be as abundant in midsummer as in late summer and autumn.

Table XI shows that scattered unworn and slightly worn queens were found in nests through the summer months. Table X shows that most but not all of these few queens were of group B; it also shows that a few not or little worn, fertilized bees with slender ovaries (group D) were found in July and August. Such bees can only be regarded as young queens produced in summer, perhaps to replace ineffective or dead overwintered queens. Figure 33 shows

TABLE X.—Indices of Wear of Females Belonging to Groups A to E During Various Months. All specimens were taken from nests (data for April were obtained in the last half of the month). Each entry consists of the mean index of wear, the extremes in parentheses, and the number of specimens examined. From May to September data are given for each half month instead of on a monthly basis.

	Mean (and extremes) indices of wear, followed by N				
	A	B	D	C	E
April	2.9(2–4)15	2.8(2–4)13	2.5(2–3) 4	3.3(2–4) 3	
May	1.5(1–3)16	2.1(1–3) 9	1.6(1–4) 8		
	3 (3) 2	2.3(2–3) 3			1 (1) 3
June	3.3(2–5) 8	2.0(1–3) 2			1.5(1–3)22
	3.6(2–5)11	1 (1) 2		2.2(1–5)13	1.8(1–5)45
July	3.2(2–4) 9	4.2(4–5) 5		3.0(2–4) 5	1.6(1–5)112
	3.6(1–5)10	3.2(2–5) 5	2 (1–3) 3	3.4(1–5) 7	2.2(1–4)58
August	4.2(3–5) 6	2.8(1–4) 5	1 (1) 3	2.8(1–4) 4	1.9(1–5)73
	4.7(4–5) 6	4.0(3–5) 3		3.2(2–5) 5	2.1(1–4)25
September	5 (5) 1		2.9(1–5) 7	3 (3) 1	2.7(1–5)17
		(4) 1	1.1(1–5)27		1 (1) 5
October			1.1(1–2)17		
November–December			1 (1) 19		

the increasing percentage of queenless nests as the season advances. No doubt sometimes the death of a queen results in death of the colony; presumably, however, she is sometimes if not normally replaced, as is regularly the case in nests of *L. rhytidophorum* (Michener and Lange, 1958).

Efforts to shed light on these problems by marking queens in the spring when they are active as pollen collectors, in the hope of later digging them from the same nests and thus gathering data on their longevity, were failures year after year. This failure was due, in different instances, to loss of marking paint, the normal high colony mortality (Figure 4) and perhaps in other factors. The possibility exists that the queens are regularly shorter lived than we have indicated above. However, as shown in Figure 22, males are not pro-

TABLE XI.—Indices of Wear of Queens of *Lasioglossum inconspicuum* with Enlarged Ovaries. Except for April, data are given for each half month instead of on a monthly basis. The data for April were obtained in the last half of the month.

Index of wear	Number of queens (groups A and B)					
	April	May	June	July	August	September
5	.....	.....	1 1	1 2	2 5	1
4	8	.....	2 7	8 7	4 3	1
3	7	4 3	4 1	3 2	4 1	.....
2	13	10 2	2 2	2 3	.....	.....
1	.....	11	1 2	1	1	.....

duced in numbers until the last half of June. Therefore it seems clear that new queens to replace overwintered individuals would not be likely to function until late June or early July. Most likely they arise as occasion demands from late June on through the summer. Queenless nests are not rare in summer as shown in Figure 33. Many queenless colonies are certainly dying but others probably

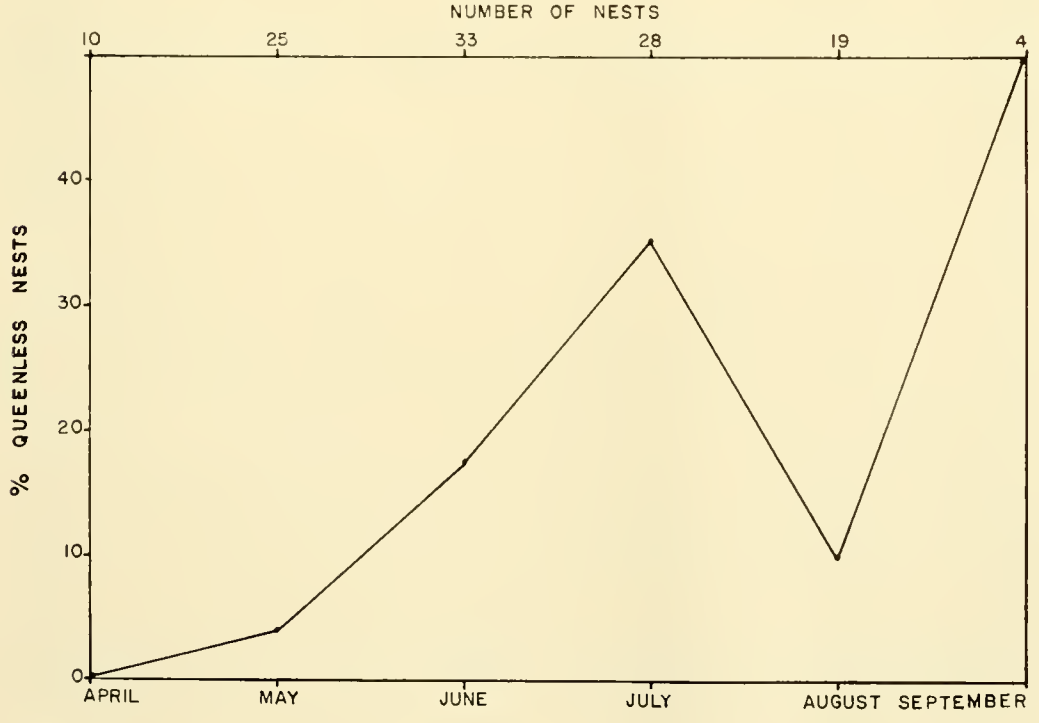


FIGURE 33. Graph showing the percentage of queenless nests in various months.

develop new queens. More specific data bearing on replacements of queens are as follows: On June 19, 1952, a nest (A) was opened that contained no queen except an unworn one of group B, with no eggs nearly ready to lay. There were neither eggs nor young larvae in the nest but there were one large larva, one prepupa, 15 female pupae and young adults still in their cells, and six unworn bees (group E) presumed to be workers. (Their wing lengths ranged from 3.04 mm. to 3.13 mm.; the queen's wing length was 3.27 mm.) During the following six days five other nests were opened; their queens were all old (indices of wear 4 and 5), of group A, and all but one of the nests had brood of all ages. It seems apparent that the original queen in nest A had been replaced, although the replacement had not yet laid her first egg, while in the other nests the overwintering queen was still active. From the above example one might suspect that group B queens are young ones developing toward the group A condition. Of course this is sometimes true but as Table X shows, group B individuals are often old and badly worn too.

Another interesting nest (B) was excavated on July 23, 1952. It contained brood of all ages and a probably overwintered, much worn (index of wear 4) queen of group A. It also contained another queen of group A and one of group B, both only slightly worn (index 2). Probably these were queens produced during the summer; possibly they replaced dead overwintered queens, but equally possibly they were additional queens. The nest also contained one fertilized worker (group D) (captured and marked as it left the nest on July 20, suggesting worker-like activities but not proving them) having one oocyte, .5 mm. long. Its index of wear was 3. In the nest also were two workers of group C and nine of group E.

On August 13, 1952, a nest (C) was opened. It contained two queens (group A) with indices of wear of 5. Possibly they were overwintered. In addition there was an individual of group D which, however, showed slight signs of general ovarial enlargement. Probably this was a young queen. In addition their were two anomalous individuals, among the half dozen summer specimens successfully dissected which were not placed in any one of the groups (A to E). They are probably best called fertilized workers but both had very irregularly enlarged ovaries. The enlargement involved chiefly one ovariole in each ovary, but the others were slightly enlarged; no oocyte approached the size or shape of a mature egg. One of these had an index of wear of 1, the other of 3. There were also 18 workers of group E.

In nest D excavated on June 24, 1954, which contained brood of all ages and three queens of group A (indices of wear 2, 4, and 4), there were also three unmated individuals included in group C. All were not or slightly worn (indices of wear 1, 1, and 2). They differed from ordinary individuals of group C in having all the ovarioles slightly enlarged, no oocyte greatly enlarged (largest .7 mm. long). They were larger than average workers (wing lengths 3.53 to 3.73 mm.). Possibly they were potential replacement queens. In addition there were thirteen probable workers of groups C and E (wing lengths 3.32 to 3.69 mm.). The largest of these was unworn and might have developed toward queenhood but one with a wing length of 3.64 mm. had an index of wear of 3.

Nest E, excavated on August 15, 1958, contained brood of various ages and one queen of group A (index of wear, 4). In addition it contained five workers. The latter had wing lengths ranging from 3.16 to 3.39 mm., while the queen was the same size as the largest worker. An additional bee was unworn with very slender ovaries; it was fertilized and therefore fell in group D. Its most remarkable feature was its size, only 2.84 mm. in wing length.

It is perhaps significant that most of the anomalous individuals discussed in the preceding paragraph occurred in nests containing relatively large populations and more than one queen. Perhaps whatever circumstances control the fate of a female function with less certainty in such nests, so that the anomalies discussed occur largely in such nests. It is obvious that such individuals are not characteristic of nests where the queen has died, leaving a group of workers some of which might in theory replace the queen functionally. Not a single caste anomaly was found in a queenless nest.

Workers: The three unworn young workers recorded for the month of May in Tables IX and X were all obtained on May 31. The number of the female bees that were classified as workers (groups C and E) is shown to fall between 77 and 86 percent for all of the summer months in Table IX. As is indicated in Table X, many of these bees which were called workers were unworn individuals that might in theory have developed into queens. That not many of those classified as group C or E in the summer months would have done so is indicated (1) by the small percentage of queens present in summer (2) by the fact that indices of wear for individuals of group E that have wing lengths less than 3.20 mm. and would therefore almost never become queens (Figure 31) average about the same as those of larger individuals that might become queens. If any large percentage of the larger individuals were being

removed from the worker class to become queens (so that they would be counted as workers only when young and unworn), the index of wear of the smallar ones classified as group E should average higher than that of the larger.

From the above it can be seen that classes A to E, while roughly comparable to similarly lettered classes of *L. rhytidophorum* (Michener and Lange, 1958), are not all identical in content. Classes A, B, and C are essentially alike for the two species. Class D as used in the present study includes overwintering females which were specifically excluded from that group in the study of *rhytidophorum.* They would have fallen in class D, however, had they not been dealt with in another way. Class E was limited by exclusion of unworn individuals in the study of *rhytidophorus.* This was necessary in order to get satisfactory data on workers because of the large percentage of queens and their presumably frequent replacement in *rhytidophorum.*

Unworn individuals placed in group E in September and October are no doubt mostly or all unmated queens that would become group D on mating.

Fertilized workers, while constituting a considerable percentage (nearly 8%) of the summer population of females of *L. rhytidophorum,* are nearly absent in *inconspicuum* during the summer. They would, of course, fall in group D. One such individual is discussed in the paragraph on nest B in the preceding section on "Queens," and one other was tentatively recognized during the summer. Of course such workers could be distinguished from young queens only if their activities were noted or if mandibular wear indicated considerable activity and age in a fertilized bee whose ovaries remained slender. Such bees were not found during the summer. In spring, however, some such bees were found as indicated in the section on "Division of Labor Among Queens in Polygynous Nests."

In September, however, fertilized workers appear in some numbers, as suggested by the high indices of wear of some individuals of group D, Table X. In a queenless nest excavated on September 17, 1952, four of eight workers were fertilized; one was unworn and might have overwintered as a queen but the others, having indices of wear of 2, 3, and 5, would not have overwintered, since overwintering bees are ordinarily unworn. On September 5, 1954, among specimens captured on flowers was one worker (out of six dissected) that was fertilized; it was collecting pollen like any field bee, and had an index of wear of 2. On September 15, 1954, five

workers (out of seven taken on flowers) were fertilized; they had indices of wear of 2 and 3. From these data one may summarize that in the late summer or fall, at the time that overwintering queens are being produced or probably shortly before, workers are produced which have certain queenlike characteristics, specifically willingness to mate. It is not surprising to find a physiological or behavioral continuum between workers and queens, since there is no clear differentiation in size or other characters either.

Two unfertilized workers were dissected and found to be anomalous for their unusual ovarian development. An individual which had ovaries like those of a group B queen but lacked sperm cells in the spermatheca was taken collecting pollen on flowers on August 5, 1954. It was classified as a group C worker. It was well worn (index of wear, 3) and quite small (wing length 3.39 mm.).

On August 23, 1954, a nest was excavated which contained brood of all ages except eggs. There were two queens of group A (indices of wear, 5) which had perhaps overwintered, and twelve workers (three group C, nine E). One of the workers (classified as group C) was peculiar in having ovaries like those of a queen of group A. Yet it was clearly unfertilized and was captured while entering the nest with a pollen load, indicating workerlike activities. This was the largest worker in the nest (wing length 3.55 mm.; others ranged from 3.21 to 3.42; the queens' wings measured 3.83 and 3.85 mm.) and had an index of wear of 4.

Since egg laying by workers is known to occur in queenless nests of *Apis* and *Bombus*, the question naturally arises as to whether workers of group C, and more especially those very unusual ones with much swollen ovaries such as described in the last two paragraphs, arise in nests which have lost their queens. The only unfertilized individual with much swollen ovaries taken from a nest was with two presumably functional queens (see preceding paragraph). As to ordinary workers of group C, one or more was found in each of 15 nests containing queens (groups A or B), and in only four nests lacking queens. It therefore seems clear that ovarian development of workers is not a result of lack of queens in the nest.

The importance of unfertilized egg-laying workers has been studied for halictine bees only by Noll (1931) who believed that most or all of the males develop from eggs of such workers. His evidence was very meager, however. No significant evidence on this matter was obtained in the present study.

Behavior of queens: Since most of the queens are produced in late summer or fall, we will discuss first the autumnal behavior of the young queens. Workers vanish entirely during September leaving the nests occupied by young queens. They do not maintain polished areas around the nest entrances, even if rain moistens the soil so that it would be easily worked. They commonly do maintain the nest entrances in their neat, constricted form, and on warm days at least as late as October 22 they are often to be seen guarding the nest with the head filling the hole, just as do guards at other seasons. We have not seen guarding in the few nests that were later found to contain only a single young queen.

During September and October both sexes may be seen sucking nectar from various flowers such as *Solidago* and especially *Aster.* Although males become less abundant on flowers as the season progresses, the young queens are sometimes very abundant on flowers in mid-October.

From October 19 to 22, 1952, by which time most of the flowers were dead, females of *L. inconspicuum* as well as other species of *Lasioglossum* were feeding on honeydew from the aphid, *Anoecia corni* Koch (determined by E. O. Essig). The bees were lapping the honeydew from the leaf surfaces of *Cornus asperifolia* on which the aphids were feeding. This was the only time that bees were seen feeding except from flowers.

By late October most of the nests become closed by rains and the bees remain inside. No nests were seen open in November. Excavation of nests in mid-November showed the overwintering queens at depths of 22 cm. and deeper. They were either in the main burrow, in short branches or in empty cells.

As indicated in the section on "Seasonal Cycle," young queens first reappear at the surface in late March or April. For a time many, at least, of them fly about and alight here and there on the soil as though looking for nesting places as described in the section on "Nest Construction." Such behavior may be seen as late as May 10, probably indicating diversity in the time when queens start their spring activity.

As already indicated, some of the queens remain in their overwintering nests and re-use them, while others establish new nests. (Observations on the manner of establishing new nests are described in the section on "Nest Construction.") Those which establish new nests do so as lone individuals while those remaining in old nests often are associated there with their sisters.

Lone queens do not make the smooth areas around their nest entrances which otherwise characterize nests of *L. inconspicuum*. Neither do lone queens appear as guards at their nest entrances. However, disturbance of the entrance with a hair or grass blade does sometimes cause a lone queen to come to the entrance, bite at the offending object, and even turn and plug the entrance with her abdomen as guards typically do (see section on "Guarding and Other Activities at the Nest Entrances"). One such queen was seen to keep a small mutillid out of her nest for an hour with her abdomen. Nests occupied in spring by two or more queens are often provided with smooth areas around the entrances, just as with the summer matrifilial colonies. In such cases guarding of the entrance occurs regularly. Workerlike activities of some queens in polygynous nests are suggested in the section on "Division of Labor among Queens in Polygynous Nests."

Because of variable (and often rainy) spring weather, the duration of the various phases of the spring activity of queens is variable. However, we have many data comparable to the following: Nest A, excavation started April 26, pollen still actively being collected on May 8, the nest closed and not recognizable on May 13, 18, and 25, reopened by one or more workers on June 1; Nest B, excavation started May 8, provisioning observed on May 13 and 15, nest closed and not recognizable on May 25 and June 8, open and at least one worker present on June 12. Such data show that after provisioning the last cell of the queen nest, the queen remains inactive in her nest for two or three weeks until the emergence of the first workers. This is an approach to the condition found in some Eurasian species in which the queen produces her offspring in discrete broods during the spring and summer (Noll 1931; Bonelli, 1948) or annually in the case of queens that live for several years (Plateaux-Quénu, 1959). In *L. inconspicuum* there is no evident cessation of activity of the queen after the appearance of the first workers in June until her summer or autumn senility.

After emergence of the workers and resumption of her activities, the queen never, so far as we know, acts as guard, nor does she collect pollen. Queens regularly have pollen as well as nectar in their crops, showing that they eat freely, as would be necessary considering their continued production of eggs. We have taken two queens (group A), one in July, one in early August, on flowers; both were apparently sucking nectar. We captured one queen (group A) as she was returning to her nest on July 21. From these data

we suspect that the queens leave the nests to feed. The paucity of such records (3 egg-laying queens out of 180 females captured in the field in June, July, and August and dissected) shows that the queens do not spend much time away from their nests and, furthermore, suggests that they may feed sometimes if not regularly on food brought to the nest by the workers. One group D female (probably a replacement queen) was taken on flowers in July.

That queens even after there are workers in their nests, continue to work with their mandibles, presumably in cell or burrow excavation, is shown by the increasing average indices of wear of queens as summer progresses (Tables X and XI). This increase is also one of the best evidences of longevity of many queens, although there is also evidence of production of new queens during the summer.

That much of the mandibular wear results from construction of cells and perhaps from the construction of the fine smooth cell lining is suggested by the fact that queens taken in April and May from old nests whose burrows were already made the previous year have mandibles just as worn as do queens that started new nests and had to dig their own burrows. Similarly for *Augochloropsis sparsilis* (Lepeletier) it was deduced by Michener and Lange (1959) that much of the mandibular wear results from cell construction. If this is true, the queens of *L. inconspicuum* probably are active in cell construction even when workers are present in the nest, since the queens' mandibles become more and more worn.

Division of Labor Among Queens in Polygynous Nests: In summer, when workers are present in the nests, we have no evidence of division of labor among queens in nests containing more than one queen. The degree of ovarian development of one queen in a nest has no obvious relation to that of another so that there may be, for example, in a digynous nest, two queens of group A, two of group B, or one A and one B.

In spring, when there are no workers, the queens in polygynous nests sometimes all have enlarged ovaries and, as Figure 18 indicates, all presumably lay eggs. Figure 18, however, is based on nests opened in May and especially in the later half of May; *i. e.,* on nests in which the production of new cells by the queens has stopped. Earlier in the spring most of the polygynous nests contain one or more "queens" that have slender ovaries (group D) or occasionally ovaries suggestive of those of workers of group C.

The fate of these overwintered individuals which are presumably potential queens is not clear. Presumably at least some of them

attain full ovarian development later. Some of them may leave their overwintering nests to establish their own new nests. However, we have repeated records of such bees collecting pollen and carrying pollen loads to their nest. Clearly in this case they are, for the time at least, functioning like workers in that they are provisioning cells in which other bees (queens of groups A and B) will lay eggs. It is probable also that it is such bees that guard the nests and make the smooth areas around the entrances since these are activities of workers in summer. It is therefore quite possible that some of the worker-like but fertilized overwintered females are short-lived like workers. Therefore their disappearance in late spring may result either from their death or from further ovarian development.

To give more completely our data on the ovarian conditions of females in polygynous nests opened in April and the first half of May, the conditions of females from such nests are indicated below in terms of groups (as defined in the section entitled "Caste Differences"), those from each nest being enclosed in separate parentheses: (AB) (AAB) (BB) (ABD) (ABD) (ABD) (AAD) (AABBDD) (BDD) (BD) (ADD) (AAAAD) (AAAD). Lone females were also occasionally in group D but the great majority of lone individuals were in groups A or B, so that most of the individuals of group D found in the spring were in the relatively few polygynous nests.

Behavior of Workers: As can be seen from Table X, the average index of wear of workers is much less than that of queens. This indicates that they do much less excavation or cell making per individual than do queens. Workers of group C have higher average indices of wear than those of group E, showing that they work more or longer in the nest than do those of group E. Individual workers of either group, however, have indices of wear as high as any queen, indicating that occasional workers do much work in the nests.

In the course of studying the duration of pollen-collecting trips by marked workers during the summer, data were also obtained on survival and other behavioral characteristics of these workers. In addition to marking foraging bees, we aspirated other bees from the nest entrances and marked them. We learned that, unlike foragers, such bees, when released, often could not find their way back to their nest. We concluded that they probably had not been out of the nest and had not learned the landmarks that would permit them to relocate their nest, and we developed a technique for re-introducing them to their nest through a glass tube after marking.

After all the bees that we could get from a nest had been marked, new ones usually appeared on succeeding days. These new workers were consistently found at the nest entrance or were sucked from the nest with an aspirator, but were not foragers. From this we concluded that the workers pass through a preforaging stage when they do not go out of the nest. During this stage they act as guards or move about in the burrow below the entrance. Bees examined in this stage have unworn mandibles, indicating that they do little or no excavating. The duration of the preforaging stage doubtless varies with temperature and other conditions. We have one record of a marked bee remaining in this stage for six days, but most bees marked as preforagers were foraging within four or five days or less; of course there is no certainty that they were captured and marked as soon as they might have been. However, in artificial glass nests in which pupae were placed, workers acted as guards during the same day that they left their natal cells.

In two experiments involving five bees, presumably young guards were transferred artificially to other nests and lived the rest of their lives there. The marked transferred preforagers were first seen as guards, later becoming foragers, and behaved throughout exactly as though they were in the proper nests. Foragers transferred to the wrong nests are not attacked so far as we know but leave the new nest and return to the proper one in a few minutes.

Several observations suggest that when the preforagers first leave the nest, they make feeding, not pollen-collecting, trips of long duration which are preceded by unusually long and elaborate orientation flights.

We have numerous records of the pollen-collecting activities of individual foragers lasting for eleven and twelve days, and one for fifteen days. Mandibular wear occurs during this stage, indicating that nest construction and foraging are more or less synchronous.

The data presented above suggest that after the worker bee leaves its natal cell it may live for about three weeks. We do have a record of one individual that was still in its nest 32 days after marking, but for at least the last ten days of this period it was the only worker in the nest and so far as we know did not leave the nest. It might well have lived longer than more active workers.

Guarding and Other Activities at the Nest Entrance: One of the noteworthy activities of worker bees (and queens in polygynous nests in the spring) is guarding. Such activity is characteristic of most or all halictine bees in which more than one individual occurs

in the same nest and is well developed in *L. inconspicuum*. Except at night and on unusually rainy days, each nest during the summer months is plugged most of the time by the head of a worker bee, which fits rather neatly into the constriction of the nest entrance. Disturbance of the guard by a fiber or grass blade, or by natural enemies such as mutillids or *Paralictus*, usually causes the guard to strike out repeatedly with open jaws at the offending object. If the disturbance continues, the guard bee turns and plugs the nest entrance firmly with the posterior two-thirds of the dorsum of the abdomen. The guard may remain in this position for a long time if the disturbance continues, for example, if a mutillid is trying to dislodge the guard. The guard braces herself very firmly in this position and one of the convenient ways to mark preforaging bees is to paint the marks on their abdomens when they hold this position. Of course when the guard is in this position, foraging bees can neither enter nor leave the nest.

Ordinarily, however, when the guard is in the usual position with head up and face flush with the soil surface, a bee flying toward the nest entrance appears to provide a stimulus that causes the guard to retreat, just before the returning bee lands, into the broader part of the burrow below the nest entrance. If two or more nests are close together, returning bees sometimes enter the wrong nest. So far as we know, no fighting occurs in such cases and the guard seems to show no ability to exclude foreign individuals of *L. inconspicuum*, which however soon leave the nest, as though they recognized their error. Guards have been seen to fight off *Paralictus*, possibly because they approached hesitatingly rather than rapidly like the *L. inconspicuum*. Guards also withdraw into the wider part of the burrow to allow departure of bees leaving the nest.

The aggressiveness of guards in defending the entrance clearly depends in part on their age. Young guards (*e. g.*, unmarked ones that appeared in nests after all other workers had been marked) are timid and often descend into the nest without blocking it with the abdomen. Guards with a day or two of experience are much more effective.

Occasionally after repeated disturbance a guard pushes earth up from beneath with the end of her abdomen and plugs the entrance. We noted particularly that this often happens when heavy rain falls on the nest.

During the middle parts of hot sunny days, guards are often not evident. A small disturbance at the nest entrances will bring them

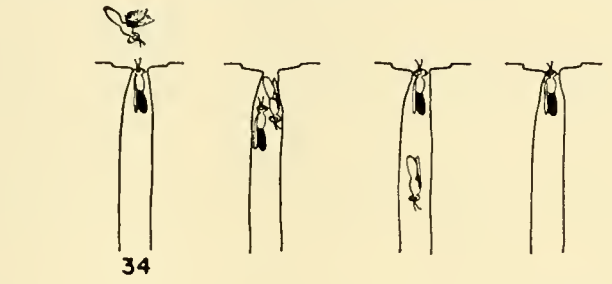
to the surface at such times, indicating that they are only a few millimeters below the entrances. Temporary shading of the nests by clouds or artificial means will also cause them to resume their positions at the surface on such days. It was found that if a thermometer resting on the soil surface registered above 125° F., the guards would not be visible at the nest entrances, but that if clouds or other shadows caused the temperature to drop to 120° F., the guards reappeared with their faces flush with the ground surface.

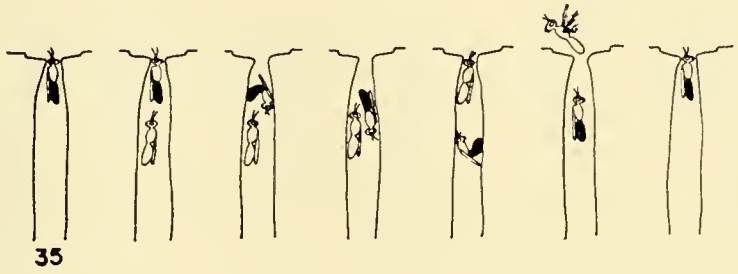
Guarding, as indicated previously, is largely an activity of preforaging workers although we have numerous records of a foraging bee spending some time as a guard, and as indicated previously, even queens may sometimes do so in the spring. Even a lone queen sometimes comes to the nest entrance at a small disturbance and may then turn and block the entrance with her abdomen, although such a queen never otherwise takes a position at the entrance as a guard. In nests containing several preforaging workers, each may take a turn as guard. We have seen such guards (marked for individual recognition) remaining at the nest entrance for periods ranging from 30 seconds to four hours, but perhaps one half to one hour is normal, after which the guard is replaced by another individual.

We were sometimes able to glimpse another bee below the guard when the latter allowed a forager to pass and were often able to suck with an aspirator a surprising number of bees from the nest entrance. To investigate the activities of bees below the nest entrances, we on various occasions and at various seasons dug a large excavation at the side of a nest and either put a piece of glass in such a position that it formed a window in the side of the upper two to four centimeters of the burrow or replaced the upper two to twenty centimeters of the burrow with a glass tube of the same diameter as the burrow. The bees came to and went from such modified nests in a normal manner providing the nest entrance proper was not destroyed and the soil on one side of the entrance was undisturbed. The observations described below were made in such situations but we have many bits of evidence indicating that they represent normal behavior. The bees in such nests were marked with colored paint for individual recognition. By making our excavation large enough to contain the observer's body, it was possible to place the eye or a lens very close to the bees themselves. Light was kept out of the glass walls of the burrows except when observations were being made.

At a nest entrance when only one bee was acting as guard, the

return of a bee from the field caused the activities shown in Figure 34. The departure of a bee to the field caused the activities shown in Figure 35. The turning of the guard shown in Figure 35 is invariable, so far as we know; bees always pass one another in the





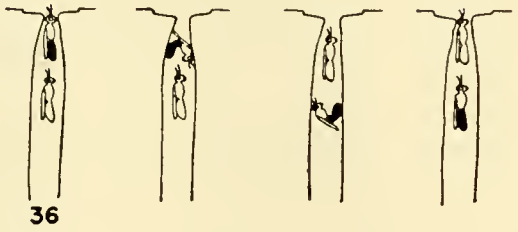


FIGURE 34. Diagrams showing how a guard draws into the burrow, behind the narrow entrance, to allow a returning bee to pass. The guard is marked with black on the abdomen.

FIGURE 35. Diagrams showing how a foraging bee passes the guard when leaving the nest. Note that the guard backs into the burrow, away from the narrow entrance, and then turns over so that the bees face one another when passing. The guard is marked with black on the abdomen.

FIGURE 36. Diagrams showing how two guard bees exchange positions. One of them is marked with black on the abdomen.

FIGURE 37. Diagrams showing activities of three guard bees (differentially marked for easy recognition) during five minutes of observation. No foragers left or returned during this period. Note that the bees sometimes turn over for unknown reasons other than to allow passing.

burrow when facing toward one another and not when facing in the same direction.

In most active nests which we studied in summer there were two or more bees spending much of their time at or near the nest entrance. If the guard were removed artificially, another bee usually replaced it immediately, for it had only to ascend to the nest entrance from a few millimeters below. The same thing can be repeated several times in nests with large populations of young workers; after the supply of young workers is exhausted it seems to take longer for the older workers to find the unguarded nest entrance and take up positions as guards.

In view of the above it was not surprising to find that several workers (usually young ones) often are in the upper part of the nest burrow. They sometimes exchange positions as guards, as indicated in Figure 36; again they pass only when facing one another. Often there is much moving up and down the burrow by bees below the guard, and a bee often turns over and over, summersault fashion, even when not passing another bee. Figure 37 shows the activities of three bees in the upper part of the nest burrow; the entire series of sketches represents a period of about five minutes of observation. Of course when a bee that is leaving the nest comes up the burrow, each of the bees above it must turn over in order to pass, as is shown for a single bee in Figure 35.

Co-operative Activity Among Workers: Division of labor among workers of various ages has already been described, younger individuals remaining in the nest and often acting as guards, older individuals serving as foragers, and sometimes also as guards. The present section presents evidence on co-operative activity among foraging workers. It is, of course, possible that each worker makes and provisions its own cells; illustrations such as Figure 14 show that each worker does not make its own branch burrow and group of cells, for there are not enough such groups. Alternatively, the workers might co-operate in making and provisioning cells, several working on one cell simultaneously.

Tentatively, we believe that such co-operative activity occurs, at least in provisioning. The number of pollen-collecting bees in a nest appears to consistently exceed the number of cells being provisioned. For example, one nest, watched continually in the morning hours, yielded four pollen collectors; on excavation in the afternoon of the same day only one partly-provisioned cell was found, plus two empty cells which the pollen collectors might theoretically have started to

provision with the pollen that they were carrying when captured. Another nest yielded seven pollen collectors; when excavated the same afternoon three partially-provisioned and four empty cells were found. A third nest yielded twelve pollen collectors; when excavated the same day two partially provisioned cells, five empty cells and two complete pollen balls in open cells without eggs were found. Such data seems to leave no doubt of co-operative activity in provisioning cells, but unfortunately we often felt that because of the extent of the nest, small size of the burrows, and often poor soil consistency, we might have missed a few cells. We do not believe that such was regularly the case, however.

A further effort to prove more decisively that workers co-operate in provisioning cells was made by marking pollen loads of returning foragers with colored powders, using different colors on different foragers which were marked for individual recognition. This proved to be a difficult technique for the foragers were much disturbed if captured; instead we blew the powder onto them just before they entered the burrow. We did find differently colored particles mixed in single pollen masses but always in such proportion that one greatly predominated and the others might have been introduced accidentally by bees that became contaminated in the burrow with powder lost from the bodies of other bees. We believe that the method may have some value for use with other species but regard it as inconclusive for such small and inconvenient forms as *L. inconspicuum.*

NEED FOR FURTHER STUDY

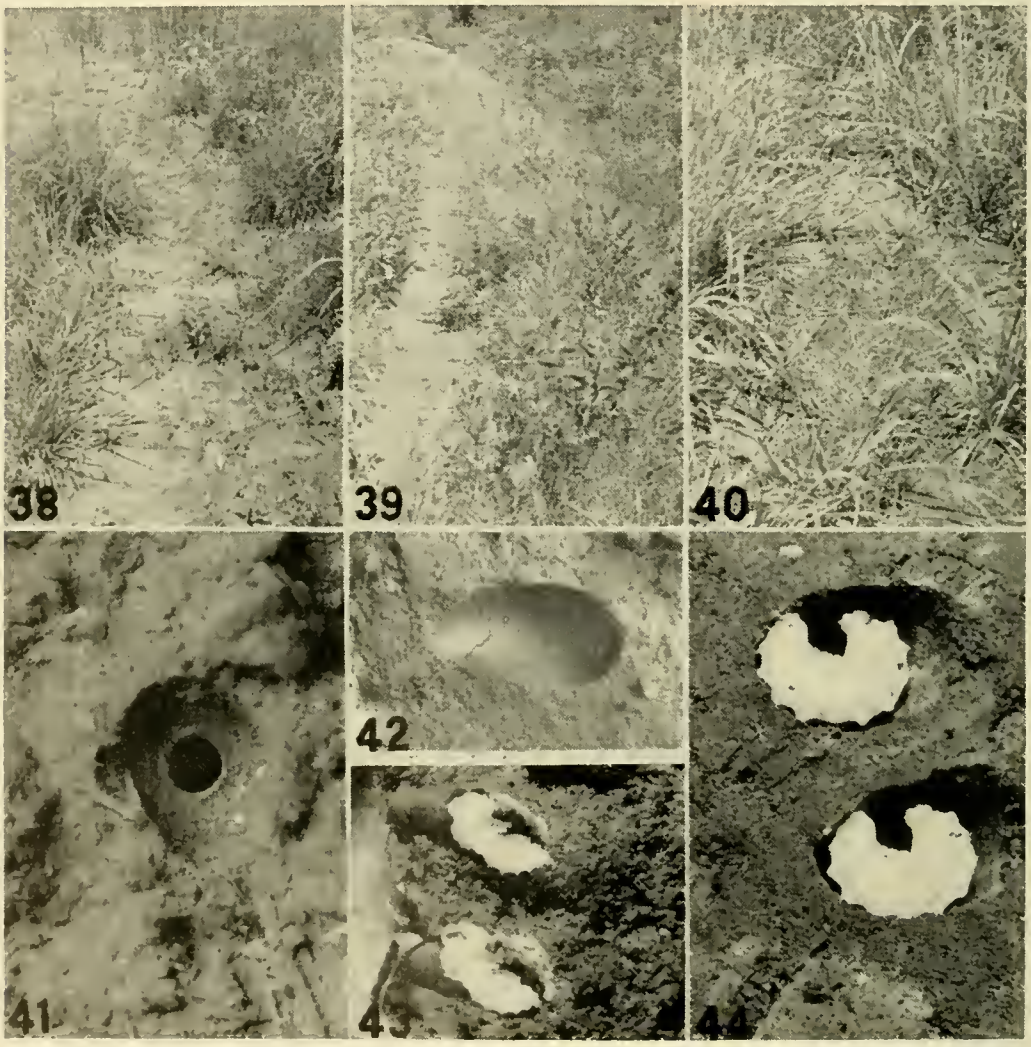
To the authors an impressive part of this study has been the enormous areas of investigation in which little or nothing is known (for this bee or for any other) in spite of a fairly intensive study. Some of these matters can be solved by additional field investigations. For example, whatever combination of temperature, light intensity, wind, and perhaps other factors determines when bees fly and when they do not could be elucidated by more field data, as could flight ranges, soil moisture requirements for survival of a colony, etc.

However, for investigation of many of the more basic aspects of social organization, our techniques have enabled us to do little more than hint at possible solutions to the problems. It is urgent that techniques be developed so that actual behavior in the nests can be seen rather than merely inferred. We need to know more about integration of members of the colony, the food sources of the queens

in matrifilial colonies (her own trips to the field, or food brought in by workers), the longevity of queens, the interactions among workers which are jointly provisioning cells, etc.

Obviously many interesting ethological observations could also be made if laboratory colonies could be established.

Another field in which more information is needed concerns the question of why some females become long-lived, sexually functional queens while others become short-lived workers. In the better known social insects the answers to this and related questions are partly known, but in primitively social insects such as *L. incon-*



FIGURES 38 to 40. Nesting places. Figure 38, Sycamore Slope; Figure 39, Prairie Road; Figure 40, Intersection.

FIGURE 41. Nest entrance, showing smooth depressed area.

FIGURE 42. Horizontal section of a cell. The scale at the bottom of the figure is in millimeters.

FIGURE 43. Pupae in cells; feces (pale) on upper distal surfaces of cells.

FIGURE 44. Prepupae in cells. The cut through both cells is oblique so that the feces scarcely show and the cell plugs are represented by only a little loose dirt at the right-hand end of each cell.

spicuum, they are quite unknown. Since caste is related to size, and size seems to be related to season (perhaps to temperature, probably not to kind of food as various acceptable pollen sources are available at all seasons), it would be interesting to rear bees under various temperature conditions (as well as with various amounts of food) and observe the behavior of the resulting adults. On the other hand, since workerlike activity can arise among presumably potential queens in polygynous spring nests, it would appear that caste determination can occur in the adult stage (as has been suggested also for *L. rhytidophorum* (Michener and Lange, 1958). If this is true, an interaction of some sort among females must be postulated, with pheromones or some other factor determining ovarian development, mating, longevity, etc. This seems unlikely among insects which seem to have so little contact with one another as members of a colony of *Lasioglossum.* Obviously an experimental approach to such problems is needed.

We have good hopes that it will soon be possible to colonize this or other halictine bees in the laboratory and that having achieved this, some of the questions enumerated above can be answered.

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